POPULATION BIOLOGY AND ECOLOGY OF THE NORTH PACIFIC GIANT OCTOPUS IN THE EASTERN BERING SEA

By

Reid S. Brewer, B.S., M.S.

A Dissertation Submitted in Partial Fulfillment of the Requirements

for the Degree of

Doctor of Philosophy

in

Marine Biology

University of Alaska Fairbanks

August 2016

APPROVED:

Brenda L. Norcross, Committee Chair
Andrew C. Seitz, Committee Member
Arny L. Blanchard, Committee Member
Olav A. Ormseth, Committee Member
Sherry L. Tamone, Committee Member
Sarah M. Hardy, Chair
Department of Marine Biology
Bradley S. Moran, Dean
School of Fisheries and Ocean Sciences
TBD, Graduate School Dean

Abstract

The North Pacific giant octopus (*Enteroctopus dofleini*) is an important member of pan-Pacific coastal ecosystems and represents a large incidental catch in Alaska; however little is known about the biology and ecology of this species, which hinders management. To improve our understanding of *E. dofleini* biology, I conducted a multiyear tagging study in a 25 km^2 study area in the eastern Bering Sea (EBS). I used Visible Implant Elastomers to determine growth and movement patterns for *E. dofleini* and sacrificed octopus were examined to determine seasonal and sex-specific reproductive characteristics. Using tagging data and Cormack-Jolly-Seber models, I estimated survival and study-area abundance for *E. dofleini* and expanded the abundance estimates to neighboring areas where most of the incidental catch of octopus occurs. In this three-year study, a total of 1,714 *E. dofleini* were tagged and 246 were recaptured. In autumn when temperatures were warmest, *E. dofleini* had higher growth rates, moved more and both sexes were predominantly mature when compared to colder winter months. Size also played a role in *E. dofleini* ecology, with smaller octopus growing faster than larger octopus and larger, mature octopus moving more than smaller, immature octopus. The abundance estimate for octopus in the study area was 3,180 octopus or 127 octopus per km^2, and annual survival was 3.33%. Using 20 years of data from the federal groundfish observer program, I estimated that the biomass for *E. dofleini* in the area where most of the incident catch occurs was 20,697 mt of octopus, an order of magnitude larger than the current biomass estimate for the entire EBS. Though the study area and the scale of the mark-recapture effort were limited, the survival and abundance estimates are from the same area where most of the octopus are incidentally captured and represent an important first step in enhancing octopus management. However, the large

estimates of biomass suggest the current management is too conservative and the estimates of survival suggest that management estimates of mortality are too low.

Table of Contents

List of Figures

List of Tables

Acknowledgements

I would like to thank each of my committee members for their advice and input into my research. Dr. Brenda Norcross, my major advisor at the University of Alaska Fairbanks (UAF), guided my research, provided feedback on manuscript preparation and submission, and was the single reason that I chose to attend UAF almost 15 years ago. Dr. Andrew Seitz (UAF) has been a wonderful mentor and confidant. Andy's quick response time in turning around manuscripts and open demeanor have made this huge undertaking seem somehow doable. Thanks for always listening and always being there for me. Dr. Arny Blanchard (UAF) has helped me to find the bigger picture in what I am doing and has spent countless hours helping me work through complicated statistics. Thanks for your time, effort and advice. Dr. Sherry Tamone at the University of Alaska Southeast provided invaluable advice in tagging efforts and working with invertebrates. Thanks Sherry for always taking the time to learn about the person behind the student. Dr. Olav Ormseth at the Alaska Fisheries Science Center in Seattle has helped me think about succinctness in writing, applications of my research to broader audiences and always gave me straightforward advice. Thanks Olav for your time and efforts in this project, I hope its application will merit some changes in your neck of the woods.

This project was conceived through the ideas of several individuals, but none more so than Zach Nehus. Zach has been a friend and confidant for the last 12 years. Zach, a commercial Pacific cod fisherman, approached me about octopus in the Bering Sea in 2004 and this work is largely a result of his observations while at-sea. Additionally, Zach allowed me to 'back-pack' on his fishing vessel to perform tagging operations for four years at minimal costs. Thanks to the crew of the F/V St. Dominick. I will never forget the smell of Pacific cod slime,

lack of sleep and cold fingers while Troy Gibson, Chaz Stockton, Keith Whittern, Dan Martello and Cheerio helped me during both tag and recover operations.

I would like to thank all of my friends and family that have helped with ideas, manuscript revisions, statistics help and just being there. Thanks to Roger Deffendall, Ellen Chenoweth, Thomas Farrugia, Missy Good, Jennifer Cedarleaf, and Lauren Wild. Thanks to the 195 octopus that gave their lives so that we know more about the reproductive seasonality of this species in the Bering Sea.

Finally, I want to thank my mother Paula Brewer, and my wife Sarah Brewer. My mom for offering to enter data, reading about the statistics that I was using or offering to read manuscripts on things about which she knew nothing. Sarah's patience, guidance and motivation have been the only reason that I was able to finally finish after all of these years. Thanks to both of you for always being there and always listening.

Funding for this project was provided by the North Pacific Research Board and the University of Alaska Fairbanks School of Fisheries and Ocean Sciences.

CHAPTER ONE

Introduction

The North Pacific giant octopus (*Enteroctopus dofleini*) is an important member of pan-Pacific benthic ecosystems occurring from California to Alaska to Japan. *E. dofleini* represents an important prey resource for commercially important fisheries resources such as Pacific cod (*Gadus macrocephalus*; Poltev and Stominok 2008) and Pacific halibut (*Hippoglossus stenolepis*; Best and St-Pierre 1986). This species is also consumed by marine mammals including sea otters (*Enhydra lutris;* Watt et al. 2000), harbor seals (*Phoca vitulina;* Conners and Jorgensen 2008), and endangered Steller sea lions (*Eumetopias jubatus*; Merrick et al. 1997). *E. dofleini* is a predator of commercially important bivalves (Dodge and Scheel 1999), crab species (Vincent et al. 1998), and many benthic fish species (Hartwick et al. 1981). In addition, *E. dofleini* represents an important commercial fishery resource in Japan, constituting a large portion of the annual 100,000 mt octopus catch (Boyle and Rodhouse 2005). Though there has never been a directed commercial fishery for *E. dofleini* in the United States, there is a significant incidental catch of *E. dofleini* in other directed fisheries, particularly the Pacific cod fishery in the Bering Sea (Conners et al. 2014).

In October 2009, in accordance with the reauthorization of the Magnuson-Stevens Fisheries Management Act, the North Pacific Fisheries Management Council required amended fisheries management plans to account for separate assessment and management of octopuses, sharks, skates and sculpins in the Gulf of Alaska and the Bering Sea/Aleutian Islands (BSAI; Conners et al. 2014). In 2011, all eight species of octopuses found in the BSAI were grouped into an "octopus complex" and managed using a quota based on the maximum historical incidental catch, with the total allowable catch (TAC) set at 150 mt (Conners et al. 2012). In

August of 2011, the octopus catch in the BSAI, which was comprised mostly of *E. dofleini* captured in pot gear, exceeded the TAC and retention of octopuses in directed fisheries was prohibited. In October of 2011, the octopus catch exceeded the overfishing limit of 528 mt and all fishing using pot gear in the BSAI was closed. As a result of the closure the remaining 1,615 mt of quota for Pacific cod was unfished, resulting in a lost opportunity cost of approximately US$ 1 million (NMFS 2012). Fisheries managers suggest that if octopus management is to be based upon biomass and mortality estimates, then species-specific methods of estimation should be explored.

Management of *E. dofleini* in Alaska has been problematic due to inappropriate survey methods. Traditional area-swept trawl methods to determine groundfish biomass are not appropriate for octopuses because 1) octopus den in rocky areas that are not surveyed because trawl nets snag, 2) octopus may have the ability to escape trawl capture, and 3) current surveys do not sample nearshore areas where many octopuses live (Conners et al. 2014). Though trawl data represent the most reliable biomass estimates for federally managed fishes and invertebrates, it is unlikely that these surveys are sufficient to capture octopuses or represent the population of *E. dofleini* that is subject to harvest (Conners et al. 2014).

Tag and recapture methods are widely used in fisheries and wildlife management practices to provide life-history information and estimate population-level parameters. Though traditional external tags are the most widely used technique to examine growth and movement patterns of cephalopods, there are several disadvantages including damage of tissues from rubbing (Kanamaru and Yamashita 1966), tag loss (Kanamaru and Yamashita 1966; Nagasawa et al. 1993), and direct necrosis of tissues (Barry et al. 2011).

New technologies are available that allow for the minimally-invasive tagging of octopuses over periods > 1 year, so that mark-recapture studies may allow population and individual-level parameter estimates of this data poor complex. Visible Implant Elastomers (VIEs) are a relatively new tagging technology that has been used effectively on freshwater fishes (Knaepkens et al. 2007), seahorses (Mattle and Wilson 2009) and penaeid shrimp (Rozas and Minello 2011). These tags are composed of a two-part liquid silicone-based material that is mixed immediately before use and is injected just below the skin of the individual to be tagged. The liquid cures into a pliable, biocompatible solid that is externally visible through most types of pigmented skin. The pliability of the cured VIEs, the small volume of material required to make a visible mark, and its tendency to occupy available space rather than displace and irritate surrounding tissue, combine to make VIEs usable in specimens smaller than most other tags can accommodate.

This study expands the knowledge of *E. dofleini* growth, movement and reproduction while suggesting that current management of octopus in Alaska is overly conservative. The first part of the present study examined the long-term effectiveness of using VIEs on *E. dofleini*. I tagged 1,714 *E. dofleini* and recaptured 246, a recapture rate of 14%, with 31 recaptures with animals at least 60 days at liberty (Chapter 2). I combined the recapture data with measurements of ocean temperature, octopus body weight and location to estimate the impacts of both temperature and octopus weight on growth and movement (Chapter 3). Using data from the same mark-recapture study, I used Cormack-Jolly-Seber models with a logistic link function to determine estimates of population size and survival of *E. dofleini* in my 25 km^2 study area (Chapter 4). Separate from the mark-recapture study, I performed laboratory-based necropsies on 195 *E. dofleini* to determine season and sex-specific maturity patterns (Chapter 5). To

conclude, I discuss the implications of this study for future octopus management, discuss the potential implications of future climate change on octopus ecology and make recommendations on future studies that would fill in the information gaps for *E. dofleini* in the eastern Bering Sea (Chapter 6).

LITERATURE CITED

Barry PD, Tamone SL, Tallmon DA. 2011. A comparison of tagging methodology for North Pacific giant octopus *Enteroctopus dofleini*. Fish Res 109, 370–372

Best EA, St-Pierre G. 1986. Pacific Halibut as Predator and Prey. International Pacific Halibut Commission. Technical Report No 21. Seattle, WA. 27pp

Boyle P, Rodhouse P. (eds) 2005. In Cephalopods: Ecology and Fisheries, Blackwell Publishing Ltd, Oxford, UK. doi: 10.1002/9780470995310.refs

Conners ME, Jorgensen E. 2008. BSAI Octopus Complex. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pac. Fish. Mgmt. Council, Anchorage, AK

Conners ME, Conrath C, Aydin K. 2012. Assessment of the Octopus Stock Complex in the Bering Sea and Aleutian Islands. North Pac. Fish. Mgmt. Council, Anchorage, AK

Conners ME, Conrath C, Aydin K. 2014. Assessment of the Octopus Stock Complex in the Bering Sea and Aleutian Islands. North Pac. Fish. Mgmt. Council, Anchorage, AK

Dodge R, Scheel D. 1999. Remains of the prey- recognizing the midden piles of *Octopus dofleini*. Veliger 42: 260-266

Hartwick EB, Tulloch L, MacDonald S. 1981. Feeding and growth of *Octopus dofleini*. Veliger 24: 129-138

Kanamaru S, Yamashita Y. 1966. The results of tagging studies of Mizudako which were carried out from 1960-1965 in the northern part of the Japan Sea. Report of the Hokkaido Marine Research Center

Knaepkens G, Maerten E, Eens M. 2007. Performance of a pool-and-weir fish pass for small bottom-dwelling freshwater fish species in a regulated lowland river. Anim Biol 57:423-432

Mattle B, Wilson AB. 2009. Body size preferences in the pot-bellied seahorse *Hippocampus abdominalis* : choosy males and indiscriminate females. Behav Ecol and Sociobiol 63:1403–1410

Merrick RL, Chumbley MK, Byrd GV. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. Can J Fish Aquat Sci 54(6):1342-1348

Nagasawa K, Takayanagi S, Takami T (1993) Cephalopod tagging and marking in Japan, a review. In: Okutani T, O'Dor RK, Kubodera T (Eds) Recent advances in cephalopod fisheries biology. Tokai University Press, Tokyo, pp 313–330

NMFS 2012. Bering Sea Aleutian Islands Catch Report through 31 December 2011, National Marine Fisheries Service

Poltev YN, Stominok DY. 2008. Feeding habits the Pacific cod *Gadus macrocephalus* in oceanic waters of the Northern Kuril Islands and Southeast Kamchatka. Russ J Mar Biol 34(5):316-324

Rozas LP, Minello TJ. 2011. Variation in penaeid shrimp growth rates along an estuarine salinity gradient: Implications for managing river diversions. J Exp Mar Biol Ecol 397:196-207

Vincent TS, Scheel D, Hough K. 1998. Some aspects of diet and foraging behavior of *Octopus dofleini* in its northernmost range. Mar Ecol 19:13-29

Watt J, Siniff DB, Estes JA. 2000. Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. Oecologia 124(2):289-298

CHAPTER TWO

Long-term retention of internal elastomer tags in a wild population of North Pacific giant octopus (*Enteroctopus dofleini*)[1]

ABSTRACT: Visible Implant Elastomers (VIEs) represent a viable approach for long-term tracking of North Pacific giant octopus (*Enteroctopus dofleini*) in Alaska. Over a three-year period, 1,714 *E. dofleini* were tagged with individually identifiable VIEs and 246 *E. dofleini* were recaptured in a 25 km^2 area. Of the 246 *E. dofleini* recaptured, 31 were at liberty for 60 days or more with a maximum time at liberty of 374 days. This study shows that long-term retention of VIEs are a vital tool in determining important life-history information for octopuses.

[1]Brewer RS, Norcross BL. 2012. Long-term retention of internal elastomer tags in a wild population of North Pacific giant octopus (*Enteroctopus dofleini*). Fish Res 134-136:17-20, doi 10.1016/j.fishres.2012.07.020

INTRODUCTION

Tag and recapture methods are widely used in fisheries and wildlife management practices to estimate life-history information and population level parameters. Cephalopods are notoriously difficult to tag for a variety of reasons (Semmens et al. 2007). Though external tags are the most widely used technique to examine growth and movement patterns of cephalopods, there are several disadvantages including damage of tissues from rubbing (Kanamaru and Yamashita 1966), tag loss (Kanamaru and Yamashita 1966; Nagasawa et al. 1993), and direct necrosis of tissues (Barry et al. 2011).

Though the North Pacific giant octopus *(Enteroctopus dofleini*) plays a critical role in both fisheries and ecosystems, 60 years of tagging experiments have met with limited success. Spaghetti tags are commonly ripped out by *E. dofleini* and often result in enlarged wounds in the tagging area (Kanamaru and Yamashita 1966). Chemical tags fade quickly and the number of tags available is limiting (Semmens et al. 2007). Cold and hot brands cause necrosis of tissues and likely death of the octopus as few, if any, are ever recaptured (Katayama and Morita 1960). Peterson disc tags quickly become occluded by octopus mantle tissue and cause necrosis of tissue around the tag (Barry et al. 2011). Acoustic tags and moored tracking systems are expensive (Semmens et al. 2007). Passive Integrated Transponder (PIT) tags and coded micro-wire tags are small enough to be non-invasive for octopus, but must be read by a portable tag reader that may not be practical for most fishing fleets (Roussel et al. 2000).

Because the retention of tags is relatively limited, fisheries and ecological information on *E. dofleini* is also limited. Few studies have directly investigated growth, reproduction or fecundity of *E. dofleini* in the wild and virtually no studies have addressed these life-history parameters in Alaska. Though there is currently no commercial fishery for *E. dofleini* in Alaska,

fisheries managers are attempting to limit the by-catch of this species by understanding population-level parameters such as movement, abundance and natural mortality. Introducing a successful tagging methodology that allows for long-term retention while minimizing impact on individuals would address these needs.

The Northwest Marine Technology Visible Implant Elastomers (VIEs) are a relatively new tagging technology that has been used effectively on species that are challenging to tag (Knaepkens et al. 2007; Mattle and Wilson 2009; Rozas and Minello 2011; Barry et al. 2011). VIEs are composed of a two-part liquid silicone-based material that is mixed immediately before use and is injected just below the skin of the individual to be tagged. The two-part liquid cures into a pliable, biocompatible solid that is externally visible through most types of pigmented skin (NMT 2010). The pliability of the cured VIEs, the small volume of material required to make a visible mark, and its tendency to occupy available space rather than displace and irritate surrounding tissue, combine to make VIEs usable in specimens smaller than most other tags can accommodate (NMT 2010). Visible Implant Elastomers have been used successfully on nine families of amphibians (Matsuda and Richardson 2005), ten families of crustaceans (Rozas and Minello 2011), fifty-six families of fishes (Knaepkens et al. 2007), and two families of mollusks, including Caribbean reef squid (*Sepioteuthis sepioidea*; Zeeh and Wood 2009) and the North Pacific giant octopus (Barry et al. 2007; Barry et al. 2011).

Over the past six years, several researchers evaluated the efficacy of using VIEs on *E. dofleini* in Alaska. In September of 2005, two aquarium-kept *E. dofleini* were tagged with VIEs. Neither showed any change in behavior or signs of impact from the tagging process and both carried the tags until their natural deaths up to two years later (R. Hocking, personal communication). In November of 2005, 41 field captured *E. dofleini* were tagged with VIEs,

though none were recaptured following three days of fishing (Wright 2008). In 2006, 125 *E. dofleini* were tagged with VIEs and three were recaptured in 33 days of fishing (Barry et al. 2011). The time at liberty for the three recaptured *E. dofleini* was 48, 52, and 63 days (Barry et al. 2007; Barry et al. 2011), thus demonstrating that VIEs are an effective approach for short-term studies of octopus.

In this study, I evaluated the long-term retention of VIEs in *E. dofleini*. The objective of this study was to evaluate the use VIEs on a wild population of *E. dofleini* over a three-year period. Long-term retention was evaluated by the longevity of recapture, and by the lack of impact of VIEs on octopus tissues. The focus of this paper will be to present information on *E. dofleini* recaptured in 60 days or more.

METHODS

This study was conducted at the edge of the Bering Sea shelf, 20 km north and east of Unalaska Island, Alaska in a 5 by 5 km area (54° 04' N, 166° 25' W; Fig. 2.1). This area and adjacent areas have been historically fished for Pacific cod (*Gadus macrocephalus*) by a local small boat fleet of three to ten vessels that frequently capture large amounts of *Enteroctopus dofleini* as non-target catch. Sampling gear was standard 2.5 x 2.5 x 0.9 m groundfish pots deployed and retrieved by an 18 m commercial fishing vessel. Each day, 100 to 200 pots were baited with Pacific herring (*Clupea pallasii*) and deployed with a minimum soak time of 12 hours. Individual pots were fished haphazardly in depths of 75 to 260 m at all hours of the day and night.

Octopus captured in pots were identified, sexed, measured, and weighed. Though there are several species of octopus in Alaska, *E. dofleini* is easily identifiable by eye papillae and size

(Jorgensen 2009). Captured octopus were sexed by distinguishing the hectocotylus on the third right arm of the males. Females were identified by the presence of suckered disks continuing all the way to the end of third right arm. After draining water from the mantle cavity, individual *E. dofleini* were weighed to the nearest 0.5 kg using Salter hanging spring scales. Each day scales were calibrated to ensure accuracy of octopus weight measurements. Octopus with damaged tissues or missing arms were not tagged.

Captured *E. dofleini* were tagged with an individual VIE sequence on the ventral surface of the mantle (Fig. 2.2). Predetermined VIE color sequences were applied with individual U-100 insulin injectors on the ventral portion of the mantle where chromatophores are less prevalent (Vidal et al. 2010). Each octopus was given a six color code that was read from left to right with the octopus arms facing away from the researcher (Fig. 2.2).

Recaptured *E. dofleini* were inspected for VIEs, measured, weighed and re-released. Upon capture, each *E. dofleini* was inspected for the presence of a VIE sequence, and if one was found, the color code was read from left to right with the arms facing away with the ventral portion of the mantle exposed. Recaptured *E. dofleini* were weighed to the nearest 0.5 kg and tag coloration and integrity were evaluated against colors standards.

To determine negative impacts of tagging protocols on octopus and tag loss, the first *E. dofleini* captured each day for twenty days was tagged with a VIE color sequence and kept in a 1 by 1 m fish tote with circulating seawater for 12 hours. At the end of the 12-hour period, these tag controlled individuals were evaluated as Excellent, Poor, or Dead and were sacrificed as part of another study (Conners et al. 2012). Octopus evaluated as Excellent were actively moving, had fewer than two injured arms, and showed an orange-red coloration. Octopus evaluated as Poor showed little to no movement, had two or more injured arms or had less intense coloration.

Octopus evaluated as Dead showed no signs of life or had severe injuries that would likely cause death. Tags were observed for signs of fading or loss of integrity that might result in future tag loss.

Fisheries managers and local fishermen were informed of the study and tag rewards were offered for recaptured octopus. Information requested included the color code identification, date, time, latitude, longitude, weight and depth. Fishermen interested in participating in the study were given logbooks and scales and were trained on how to perform weight measurements while under way. Local fishermen were actively fishing in the study area during the pot *G. macrocephalus* seasons spanning from September to November and January to March.

RESULTS

Over a period of three years, 1,714 *Enteroctopus dofleini* were captured, tagged and released from 5,163 groundfish pots. A total of 246 *E. dofleini* (14%) were recaptured and of those, 31 were at liberty for 60 days or more. The mean size of newly captured *E. dofleini* was 14.1 kg ± 0.1 SE and ranged from 1 to 30 kg. The mean time at liberty for those 31 *E. dofleini* was 179.2 ± 21.4 days with a maximum of 374 days. Individual *E. dofleini* recaptured at 60 days or more showed no signs of damage as a result of the VIEs and appeared as active as newly captured octopus. Tag readability was consistently good for all recaptures and showed no signs of wear, fractionation or fading. Each of the 20 tag controlled individuals kept for 12 hours were rated as excellent and also appeared as active as newly captured octopus.

DISCUSSION

This study demonstrates the long-term retention of VIEs in a wild population of *Enteroctopus dofleini*. These tags allowed for the tracking of many individuals over periods of over a year allowing for the estimation of population and life history parameters. The application of these tags did not directly impact individual behavior and tagged octopus recovered after long periods of time did not show any signs of necrosis or rejection of the tags.

Though longevity in tagging studies is often reported as the maximum time between tag and recapture, this result does not account for the time at liberty for the remaining recaptures. Studies using external tags on *E. dofleini* report recaptures of up to a year, while the number of individuals recaptured in 60 days or more was usually limited to one or two individuals (Kanamaru and Yamashita 1969; Robinson and Hartwick 1986; Barry et al. 2011). For VIEs, the current record between tag and recapture of *E. dofleini* is 63 days with only one individual ever recaptured in 60 days or more (Barry et al. 2007; Barry et al. 2011). In this study, the large number of *E. dofleini* recaptured in 60 days or more reflects a longer-term retention of VIEs than has been found with either external tags or other studies using VIEs. Recapturing a large number of individuals over long periods of time may be instrumental in understanding the dynamics of local populations such as estimating biomass and natural mortality. Long-term recaptures can also give insight into life-history information such as seasonal abundances, horizontal displacement or growth.

Though most studies attempt to reduce measurement variance, even the most precise protocols in the field are susceptible to errors. In tag and recapture studies, errors in weight measurements upon initial capture or at recapture can result in biased data collection for life-history information like *in situ* growth. In short-term tagging studies, these errors can show too

little or too much growth for individuals that may negate or exaggerate the actual growth experienced by the individual. Though these same errors may occur in long-term studies, the increase in temporal longevity and resultant increase in growth will reduce the impact of the error on the actual growth experienced. Though *E. dofleini* are thought to have dramatic growth rates, Robinson and Hartwick (1986) report that growth varies by size and sex, and in winter months growth may slow to zero or even show negative growth. In this study, the error of weight measurements using daily weight calibrations was estimated to be ± 0.5 kg of the actual weight of the octopus. In Barry et al. (2011), the longest time between VIE tag and recapture was 63 days with an increase in weight of 1.25 kg. If this individual had a similar 0.5 kg error as determined in this study, the actual change in weight would be between 0.75 and 1.75 kg, an error equaling 29 to 67% of the actual change in weight. The longest recapture in this study was 374 days with an increase in weight of 10 kg. Considering the same 0.5 kg error, the actual change in weight would be between 9.5 to 10.5 kg, with an error equaling 4.8 to 5.3% of the actual change in weight. Thus, short-term tagging studies may be hindered by errors associated with field measurements, given the variability or octopus growth with size, sex and temperature. Because VIEs have potential as the basis for documenting important life-history information of octopus over longer periods of time, they may be used to more accurately document changes over the life of the individual.

The lack of impact from tagging protocols has shown that VIEs may be a more reliable tagging method than external tags historically used for this species. Wounds around puncture holes from spaghetti tags increased in size over time and likely led to tag loss caused by rubbing or manual removal attempts (Kanamaru and Yamashita 1969; Nagasawa et al. 1993). Though Peterson disk tags were reported to have met with some success in Canadian studies (Robinson

and Hartwick 1986; Cosgrove 1987), Barry et al. (2007) suggest that these tags can irritate surrounding tissues leading to necrosis and tag loss in as little as 35 days. Visible Implant Elastomers are non-invasive, biocompatible solids that are subcutaneous and therefore are unavailable for manual removal. In this study, none of the recaptured *E. dofleini* showed any negative signs of impact from tagging and each recaptured individual behaved similar to newly captured octopus. Fishermen reported no problem identifying or reading VIEs. Consistent reports of brightly colored tags were reported throughout this study so that color fading did not appear to be an issue even over this extended period of time. The condition of the 20 *E. dofleini* kept as tag controls was excellent after 12 hours, which suggests that both tagging mortality using VIEs and discard mortality for pot-captured octopus is low.

ACKNOWLEDGEMENTS

This study was supported by the North Pacific Research Board projects 906 and 1005, Alaska Sea Grant and National Oceanic and Atmospheric Administration. I would like to thank Andy Seitz, Sherry Tamone, Olav Ormseth and Arny Blanchard for reviewing this manuscript. I am also grateful to Zach Nehus, Chaz Stockton, Keith Whittern, and Troy Gibson for assistance in the field. Logistics and recapture support provided by the crew of the F/V St. Dominick.

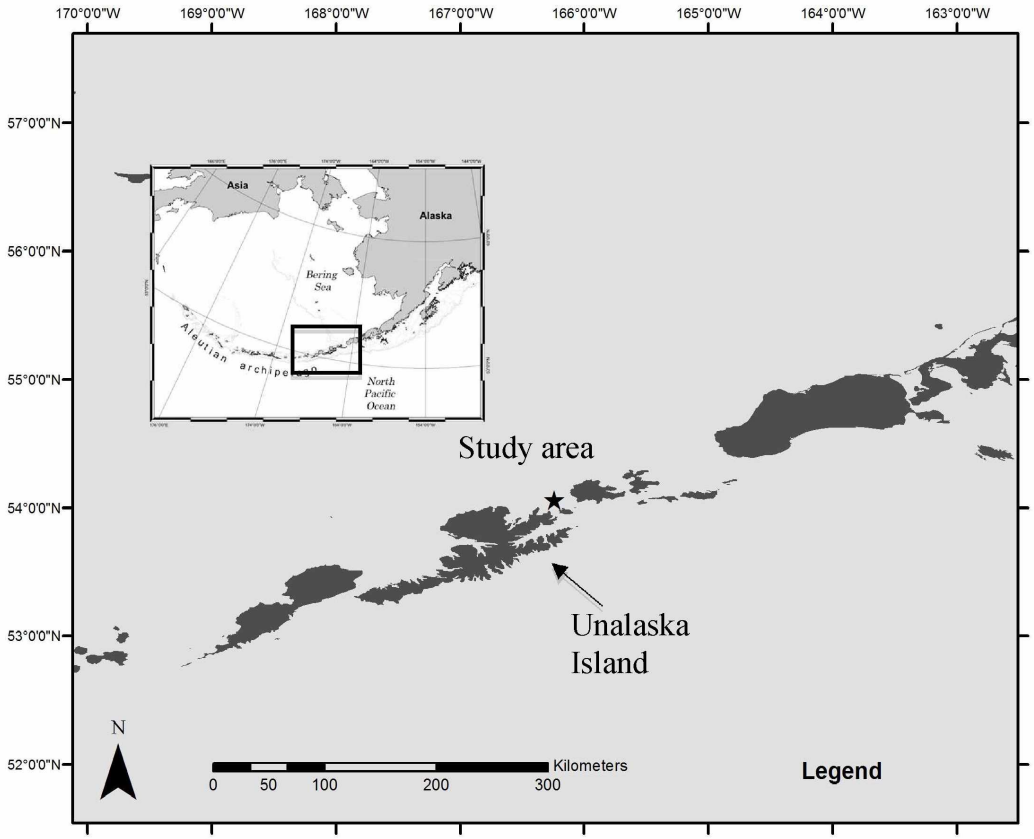


Figure 2.1. Map of Unalaska Island and the study area. The area fished was approximately 5 by 5 km

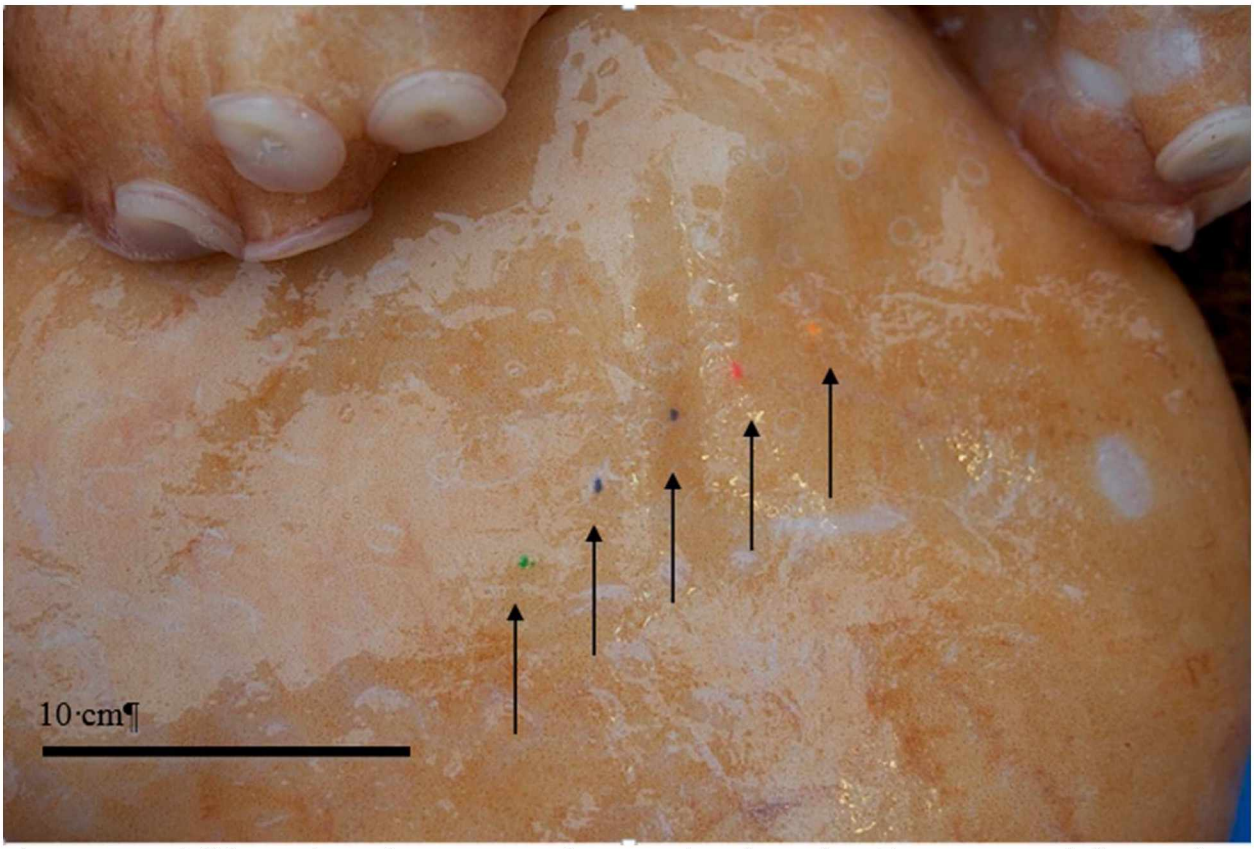


Figure 2.2. Visible Implant Elastomers on the ventral surface of an *Enteroctopus dofleini*. The sequence is read from left to right with the arms facing away. This photo was taken from an octopus that was recaptured after 186 days and the tag reads green, blue, blue, red, orange. Arrows indicate tag positions

LITERATURE CITED

Barry PD, Brewer R, Browning J, Grund J, Scheel D, Tallmon D, Tamone S. 2007. AFDF Final Report. Investigation of tagging methods and tracking for Giant Pacific Octopus (*Enteroctopus dofleini*) in Southcentral Alaska. Award Number: COBS: NA04NMF4540379

Barry PD, Tamone SL, Tallmon DA. 2011. A comparison of tagging methodology for North Pacific giant octopus *Enteroctopus dofleini*. Fish Res 109:370-372

Conners ME, Conrath C, Aydin K. 2012. Assessment of the Octopus Stock Complex in the Bering Sea and Aleutian Islands. North Pac. Fish. Mgmt. Council, Anchorage, AK

Cosgrove, JA. 1987. Aspects of the natural history of *Octopus dofleini*, the Giant Pacific Octopus. MS thesis, University of Victoria, British Columbia

Jorgensen EM. 2009. Field guide to Squids and Octopods of the Eastern North Pacific and Bering Sea. Alaska Sea Grant College Program, University of Alaska Fairbanks

Kanamaru S, Yamashita Y. 1966. The results of tagging studies of Mizudako which were carried out from 1960-1965 in the northern part of the Japan Sea. Report of the Hokkaido Marine Research Center

Kanamaru S, Yamashita Y. 1969. The Fishery Biology of the Octopus, "Mizu-dako" Summer Movement in Onishika Area of North-western part of Hokkaido. Report of the Hokkaido Marine Research Center

Katayama K, Morita S. 1960. Preliminary survey of common octopus. Annual Report. Okayama Prefectural Fisheries Experimental Station

Knaepkens G, Maerten E, Eens M. 2007. Performance of a pool-and-weir fish pass for small bottom-dwelling freshwater fish species in a regulated lowland river. Anim Biol 57:423-432

Matsuda BM, Richardson JS. 2005. Movement patterns and relative abundance of coastal tailed frogs in clear cuts and mature forest stands. Can J of For Res 35:1131-1138

Mattle B, Wilson AB. 2009. Body size preferences in the pot-bellied seahorse *Hippocampus abdominalis*: choosy males and indiscriminate females. Behav Ecol and Sociobiol 63:1403–1410

Nagawasa K, Takayanagi S, Takami T. 1993. Cephalopod tagging and marking in Japan, a review. In: Okutani T, O'Dor RK, Kubodera T (Eds) Recent advances in cephalopod fisheries biology. Tokai University Press, Tokyo, pp313–330

NMT 2010. Visible Implant Elastomer Tags (VIE). http://www.nmt-inc.com/products/vie/vie.htm. Accessed 16 April 2011

Robinson SMC, Hartwick EB. 1986. Analysis of growth based on tag-recapture of the Giant Pacific octopus *Octopus dofleini martini*. J Zool Lond 209:559-572

Roussel JM, Haro A, Cunjak RA .2000. Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. Can J Fish Aquat Sci 57:1326–1329

Rozas LP, Minello TJ . 2011. Variation in penaeid shrimp growth rates along an estuarine salinity gradient: Implications for managing river diversions. J Exp Mar Biol Ecol 397:196-207

Semmens JM, Pecl G, Gillanders B, Waluda C, Shea E, Jouffre D, Ichii T, Zumholz K, Katugin O, Leporati S, Shaw P. 2007. Approaches to resolving cephalopod movement and migration patterns. Rev Fish Biol Fish 17:401-423

Vidal EAG, Fuentes L, da Silva LB. 2010. Defining *Octopus vulgaris* populations: A comparative study of the morphology and chromatophore pattern on paralarvae from Northeastern and Southwestern Atlantic. Fish Res 106:199-208

Wright SE. 2008. Nearshore marine research in Alaska (VII): Final comprehensive progress report. NOAA Cooperative Agreement NA05NMF4371059: 2-8

Zeeh KM, Wood JB. 2009. Impact of visible implant elastomer tags on the growth rate of captive Caribbean reef squid *Sepioteuthis sepioidea*. Fish Res 95:362-364

CHAPTER THREE

Temperature and size-dependent growth and movement of the North Pacific giant octopus (*Enteroctopus dofleini*) in the Bering Sea[1]

ABSTRACT: Octopus growth and movement occur during all life stages and have implications for survival, food web dynamics, and reproduction. From 2009 to 2011, I tagged 1,714 North Pacific giant octopus (*Enteroctopus dofleini*) in the eastern Bering Sea with Visible Implant Elastomers to better understand the ecology of this data-poor species. Over this period, 246 of the tagged individuals were recaptured. In autumn when temperatures were warmest, *E. dofleini* had higher growth rates and moved more than in colder winter months. For both short and long-term recaptures, small octopus grew faster than large octopus. Movement over short and longtime periods was low for very small and very large octopus and high for median sized octopus, which is likely a function of maturity status and reproductive activities. Many of the octopus were recaptured less than 2 km from the initial tagging location for time periods up to a year, suggesting long-term site fidelity. As temperature and size may be tightly linked to growth and movement rates for *E. dofleini* in the eastern Bering Sea, predicted climate warming will likely alter ecological processes for the species and impact their distribution.

[1]Brewer RS, Norcross BL, Chenoweth E. Submitted. Temperature and size-dependent growth and movement of the North Pacific giant octopus (*Enteroctopus dofleini*) in the Bering Sea. Mar Biol Res

INTRODUCTION

Growth and movement are key aspects of octopus ecology because they are direct indicators of energy utilization (Andre et al. 2009), influence the success of reproductive efforts, (Semmens et al. 2004) and may determine trophic interactions with other species. Octopuses are known to have very high food consumption rates (Gillespie et al. 1998), high energy conversion rates (Robinson 1983; Hartwick et al. 1981), high metabolic rates (Rigby and Sakurai 2004), and an uncommon ability to sustain continuous muscle growth (Semmens et al. 2004). These characteristics allow octopus to maintain high growth rates (Andre et al. 2009) and have large usage areas (Scheel and Bisson 2012) during relatively short lifespans.

Though it is often characterized as rapid, non-asymptotic and highly variable, octopus growth is not well understood (Semmens et al. 2004). Growth is an important aspect of octopus ecology as it allows for refugia from predation (Mather and O'Dor 1991), impacts size at maturity (Wood and O'Dor 2000), and increases mating potential (Semmens et al. 2004). Biotic and abiotic factors can modify growth in cephalopods, including temperature (Forsythe 1993), food availability (Castro and Lee 1994), and food quality (Hamazaki et al. 1991).

Growth is usually determined by measuring the increase in whole-animal weight, though traditional methods of measuring growth have proven difficult for most cephalopod species. Modal progression analysis is not suitable for cephalopods, as the age of cohorts has not been validated (Cortez et al. 1999). Biochemical markers of instantaneous growth show no consistent relationship with octopus growth in captive studies (Pierce et al. 1999). Likewise, the analysis of growth increments in hard structures gives limited information due to wear on beaks with age (Hernandez-Lopez et al. 2001). Histological quantification of lipofuscin in nervous tissues proportional to age has yet to be validated using known-age animals (Doubleday and Semmens

2010). Finally, mark-recapture studies are rare and have low retention rates for traditional externally attached tags (Domain et al. 2000). Regardless of the assessment used, octopus growth is poorly understood and methods for understanding growth have not been standardized.

As mark-recapture studies have limited success, little is known about octopus movement patterns. Movement is necessary for foraging success (Hartwick et al. 1984), predator avoidance (Semmens et al. 2007), and/or mate selection (Conrath and Conners 2014). Cephalopod movements have been examined using tag-recapture studies, electronic tags, chemical tags, natural tags and tracking fishing fleets with satellite data (Semmens et al. 2007). Similar to the challenges reported for growth, there are no standardized assessments for octopus movement and most studies employ different protocols.

Growth and movement of the North Pacific giant octopus (*Enteroctopus dofleini*) have been studied throughout the Pacific Ocean, yet this work has resulted in sparse data that are widely separated in space and time. In the 1960s, mark-recapture studies near Hokkaido, Japan found that *E. dofleini* grew from 1 kg to 10 kg in a single year (Mottet 1975) and that juvenile octopus made seasonal inshore-offshore migrations up to 50 km in some areas (Kanamaru and Yamashita 1966; Sato and Yorita 1999). In the 1980s, mark-recapture studies in British Columbia found that *E. dofleini* grew at a rate of up to 2% of their body weight per day (Hartwick et al. 1981), maintained site longevity for up to 6.5 months (Hartwick et al. 1984), had rapid growth occurring in warmer months and slow growth occurring in colder months, and did not make seasonal migrations as reported in Japan (Robinson and Hartwick 1986). In the 2000s, mark-recapture studies in Prince William Sound, Alaska did not recapture enough *E. dofleini* to estimate growth (Barry et al. 2007), and found that though individuals used large areas (up to 50

km^2 for 20 days of tracking), there was no evidence for seasonal migrations (Barry et al. 2007; Scheel and Bisson 2012).

Though studies from Japan, British Columbia and Prince William Sound represent the core knowledge of *E. dofleini*, the methods used may bias some critical findings. In all of these studies, octopus arms or mantles were punctured with external tags, they released octopus at locations different from their capture, and primarily tagged immature octopus. External tags damage individuals by rubbing muscle or skin, and can create enlarged wounds in the tagging area, ultimately leading to tag loss (Kanamaru and Yamashita 1966). Alternatively, external tags can trigger occlusions of skin over the tags in as little as five weeks, causing tissue necrosis and tag loss (Barry et al. 2011). In both cases, damaged tissues may impact the behavior or physiology of individuals, which may influence the conclusions drawn from tagging studies. As *E. dofleini* use unique habitat characteristics to navigate to known den sites (Scheel 2002), relocating individuals to other areas may impact movement patterns as octopus must move to find new suitable habitats. Finally, because immature octopus are not yet producing gonads and are susceptible to predation by large fish, growth is likely focused on somatic tissues and movement is likely influenced by the constant threat of predation (Mather and O'Dor 1991).

Enhanced knowledge regarding *E. dofleini* ecology is important for understanding the role of this species in the ecosystem and for informing octopus conservation and management. Recent advances in tagging technologies allow for the collection of important ecological information, such as growth and movement, without the negative impacts often associated with external tags. Therefore, the goal of this study was to use a minimally-invasive tagging method to examine seasonal attributes of growth and movement of *E. dofleini* in the eastern Bering Sea. The specific objectives were 1) to determine short and long-term estimates of growth and

movement, and 2) to determine the role of temperature in growth and movement for this species at the northern extent of its range. Different from previous studies on *E. dofleini*, this study investigates growth and movement patterns by using a large number of tagged and recaptured individuals monitored over several years with a minimally-invasive technology. Though the present study is not broad enough to estimate growth and movement attributes for this species throughout the entire Bering Sea, the estimates presented here should prove useful in the study area, and potentially in surrounding areas, and may serve as a benchmark for further studies.

METHODS

During five seasonal periods from October 2009 to November 2011 (Table 3.1), *Enteroctopus dofleini* were captured, tagged, released and recaptured in a 25 km^2 study area approximately 20 km northeast of Unalaska, Alaska (center of study area at 54° 04' N, 166° 25' W; Fig. 3.1). The five tag/recapture trips occurred in autumns of 2009, 2010, and 2011 and winters of 2010 and 2011. Autumn sampling took place between September and November and winter sampling took place between January and March (Table 3.1).

The study area was adjacent to the edge of the Bering Sea shelf, approximately 20 km northwest of Akutan Pass, a narrow shallow channel that allows the transfer of water between the Gulf of Alaska and the Bering Sea. Mixing in Akutan Pass creates a productive ecosystem that supports a diverse array of marine organisms and commercial fisheries for several species, including Pacific cod (*Gadus macrocephalus*) and Pacific halibut (*Hippoglossus stenolepis*; Johnson 2003). Simultaneously, the strong water movement scours the bottom resulting in a bottom substrate composed of a mix of sand, gravel and boulder rubble in depths of 45 to 260 m.

Octopus were captured in 2.5 x 2.5 x 0.9 m groundfish pots during the commercial fishery for Pacific cod. Each day, 100 to 200 pots baited with Pacific herring (*Clupea pallasii*) were deployed at varying depths throughout the study area from an 18 m commercial fishing vessel. Pots were fished at all hours of day and night with a minimum soak time of 12 hours.

Bottom water temperatures were recorded continuously throughout each tagging/recapture season using HOBO TidbiT data loggers (Onset Computer Corp., Massachusetts USA). Ten TidbiTs were attached to randomly selected groundfish pots and temperature was recorded in degrees Celsius every hour that the pot was in the water. All temperatures recorded for a given month were averaged (± SE) to determine mean monthly bottom water temperature.

E. dofleini captured for the first time were sexed, weighed, tagged and released. Octopuses were identified as *E. dofleini* by observing two suckers per row down each arm, presence of papillae over both eyes, and mantle texture in longitudinal rows (Jorgensen 2009). Sex was determined by identifying the presence of a hectocotylus on the third right arm of males and its absence in females (Pickford 1964). After draining water from the mantle cavity, each octopus was weighed to the nearest 0.5 kg using a hanging spring scale. Scales were calibrated each day using calibration weights to ensure accurate weight measurements accounting for sea-state. Individuals were marked with a unique six-color code sequence using Northwest Marine Technologies Visible Implant Elastomers (VIEs; Chapter 2). The entire marking procedure took less than one minute and octopus were returned to the ocean within five minutes of removal from the water. Video cameras attached to a subsample of 15 *E. dofleini* showed that octopus released from fishing vessels did not travel a significant distance horizontally during their descent to the

seafloor, and likely returned to the same approximate location of their capture (Brewer, unpubl. data). Capture location, depth, date, and time of day were recorded for each tagged individual.

Recaptured *E. dofleini* were identified using unique VIE sequences, sexed, weighed and re-released. Visible implant Elastomers were also evaluated for tag integrity and color fading. Recapture measurement followed the protocols described for octopus at initial capture. One researcher measured and tagged all *E. dofleini* captured and three trained individuals performed recapture measurements.

Metrics of growth and movement were evaluated for each recaptured individual. To assess octopus growth rates, change in weight was used because weight is considered the most reliable indicator of octopus size (Domain et al. 2000). Growth was calculated as specific growth rate (SGR) as described by Kaufmann (1981) and Perez et al. (2006):

$$SGR = \frac{(\ln Wt2 - \ln Wt1)}{\Delta t} * 100$$

where Wt2 and Wt1 are the weights of octopus in kilograms at recapture and capture respectively and Δt is change in time in days.

As VIEs did not report real-time information on position of marked octopus, horizontal displacement between capture and recapture locations was used as a metric for movement. Horizontal displacement was calculated as the mean distance moved per day (km d^{-1}) by dividing the great circle distance between the tagging and recapture locations by the total time at liberty (days). Horizontal displacement will henceforth be referred to as movement unless otherwise noted.

Specific growth rate and movement were analyzed separately for short-term and long-term periods. Short-term recaptures were defined as octopus tagged in one season and recaptured in that same season during that same year less than 60 days post-release. Long-term

recaptures were defined as octopus tagged in one season and recaptured in a subsequent season(s), and were at liberty for at least 60 days. To explore possible predictors of short and long-term growth, a non-linear regression was performed with log-transformed growth as a response variable and year, sex, temperature and size at initial capture as explanatory variables. To explore possible predictors of short and long-term movement patterns, a Generalized Additive Model (GAM) was used with log-transformed movement as a response variable and year, sex, temperature, and size at initial capture as explanatory variables. The chosen models were the most parsimonious for explaining growth and movement and had the minimum Akaike Information Criterion (AIC). Statistical analyses of data were conducted in R (R Development Core Team 2010), with alpha = 0.05, and means reported with ± SE unless otherwise noted.

Because there are many factors that can cause individuals to show negative or zero growth (i.e., short time-at-liberty, illness, parasitism, injury), only those *E. dofleini* that showed positive SGR were considered for the growth and movement analyses (Hartwick et al. 1988). Of the 214 *E. dofleini* recaptured for the first time, 118 had a mean time at liberty of less than seven days and showed negative or zero growth, thus were discarded from analyses. Of the remaining 96 recaptures, 71 were used for short-term analysis and 25 were used for long-term analysis.

RESULTS

Capture and recapture

A total of 1,714 individual *Enteroctopus dofleini* were tagged from October 2009 to November 2011, with a mean weight of 14.1 kg ± 0.1 (Table 3.1). The depths at initial capture ranged from 75 m to 260 m with a mean depth of 106.1 m ± 0.6. The male:female sex ratio of

approximately 2:1 was consistent among the five study periods (Table 3.1). None of the VIEs observed on recaptured octopus showed missing tags or signs of color fading.

Of the total 246 recaptures, 186 were recaptured once, 24 were recaptured twice and four were recaptured three times, resulting in a recapture rate of 14%. The depth of recaptures ranged from 45 m to 202 m with a mean of 101.2 m ± 1.3. The male:female sex ratio of recaptures was 5:1. The mean weight of *E. dofleini* at first recapture (i.e. not including multiple recaptures) was 14.5 kg ± 0.2 (n = 214).

Bottom temperatures in the study area ranged from 3.53°C to 6.41°C with temperatures warmer in autumn than in winter. In autumn, bottom temperatures ranged from 5.11°C in September to 5.81°C in November with a mean of 5.31°C ± 0.01, while winter temperatures ranged from 4.74°C in January to 3.53°C in March with a mean of 4.16°C ± 0.02.

Short-term growth and movement

For short-term recaptures, temperature and size at initial capture were significant predictors of growth and movement. The mean SGR for short-term recaptures was 0.75% d^{-1} ± 0.09. SGR was positively related to temperature (Non-linear Least Squares, $t = 4.34$, $p < 0.001$; Fig. 3.2) and negatively related to size at initial capture (NLS, $t = -2.74$, $p = 0.008$; Fig. 3.3). Movement was also positively related to temperature (NLS, $t = 2.58$, $p = 0.012$; Fig. 3.4), but was greater at median sizes and reduced in very small and very large octopus (Generalized Additive Model, $F=2.52$, $p = 0.046$; Fig. 3.5). The movement for short-term recaptures ranged from 0.03 km to 4.62 km with a mean displacement of 0.96 km ± 0.12 (n = 71).

Long-term growth and movement

For long-term recaptures, size at initial capture was a significant predictor of growth and movement. The mean SGR for long-term recaptures was 0.20% d^{-1} ± 0.03 and SGR was negatively related to size at initial capture (NLS, $t = 6.74$, $p < 0.001$; Fig. 3.6). Similar to short-term recaptures, *E. dofleini* showed increased movement at median sizes and decreased movement for very small and very large octopus (GAM, $F = 2.52$, $p = 0.046$; Fig. 3.5). The total displacement distance for long-term recaptures ranged from 0.95 km to 11.5 km with a mean displacement of 2.14 km ± 0.56 ($n = 25$). Long-term recaptures moved greater distances than short-term recaptures (NLS, $t = 2.58$, $p = 0.012$).

DISCUSSION

Enteroctopus dofleini may be sensitive to environmental changes, such as unprecedented warming occurring in northern latitudes, as it has some life history attributes that are closely correlated with temperature. *E. dofleini* growth and movement increased with increasing temperatures and decreased with increasing size. For many species of octopus, changes in environmental attributes may impact growth and movement, and could have physiological and developmental consequences ultimately affecting the distributions, abundances and ecological niches of these species (Boyle and Knobloch 1982; Cortez et al. 1999; Storero et al. 2010).

The positive relationship between octopus growth and temperature is likely due to a combination of direct and indirect effects. Increases in temperature as small as 1°C may have significant positive impacts on the growth of benthic octopuses (Andre et al. 2009). In this study, the mean autumn temperature, which correlated with higher growth rates of *E. dofleini*, was warmer than mean winter temperatures. Increased growth with warmer temperatures has been observed for *E. dofleini* in British Columbia (Robinson and Hartwick 1986), *Eledone*

cirrhosa in Scotland (Boyle and Knobloch 1982), *Octopus cyanea* in Hawaii (Wells and Wells 1970), *O. maya* in Hawaii (Van Heukelem 1976), *O. mimus* in Chile (Cortez et al. 1999), *O. tehuelchus* in Patagonia (Storero et al. 2010), and *O. vulgaris* in France (Mangold and Boletsky 1973). The cause of increased growth with warmer temperatures may be a function of one or a combination of increased metabolism, food intake or food availability. In laboratory experiments with *E. dofleini*, respiration and metabolism increased while increasing temperature from 5°C to 8°C (Rigby and Sakurai 2004). For *O. briareus*, a tropical species, food intake doubled when temperatures increased from 20°C to 30°C (Borer and Lane 1971). For *E. dofleini* in British Columbia, increased growth during warmer months may be a function of food supply as octopus growth was high when the mean number of red rock crabs (*Cancer productus*) was high (Robinson and Hartwick 1986). In the colder temperatures of winter when the number of Red rock crabs decreased, growth also decreased.

Higher growth rates observed in smaller octopus may result from ontogenetic changes in the allocation of energy resources. In this study, for both short-term and long-term recaptures, smaller octopus grew faster than larger octopus. Lower growth rates with increased size have also been reported for *E. dofleini* in British Columbia (Hartwick et al. 1981), *E. megalocyathus* in Chile (Perez et al. 2006), *O. mimus* in Chile (Cortez et al. 1999), and *O. vulgaris* in Tunisia (Jabeur et al. 2012). Additionally, growth models normally demonstrate negative relationships between size and growth rate at higher sizes/ages if growth is determinate (Von Bertalanffy 1950). The decline in growth with larger size for octopus suggests that growth is determinate, although adjusted latitudinally via environmental controls. As cephalopods grow and begin to mature, allocation of energy towards reproduction increases relative to the allocation of energy to somatic growth (Semmens et al. 2004). In the present study, the mean size of 14.1 kg suggests

that a majority of the octopus examined were mature or maturing and potentially limiting investment in somatic growth.

Increased movement with temperature is likely a function of the seasonal reproductive ecology of *E. dofleini*. Temperature-dependent movement and distribution of octopus has been observed for *E. dofleini* in British Columbia (Hartwick et al. 1984), *O. vulgaris* in Greece (Katsanevakis and Verriopoulos 2004) and *O. tehuelchus* in Argentina (Iribarne 1991). In the eastern Bering Sea, mature female and male *E. dofleini* are present during warmer autumn months and only mature males are present during colder winter months, suggesting mating in autumn and winter spawning by females (Chapter 5). As part of *E. dofleini* reproductive ecology, individuals must find mates, males must inseminate females, and females must find suitable denning habitats for spawning, all of which require increased movement. In this study, 82% of the octopus captured were over 10 kg and likely mature and searching for mates. The timing for autumn mating (Chapter 5), and hence movement, may be important for the six-month development of eggs and later release of paralarvae during productive spring and summer months.

Maturity and reproduction may affect the extent of movement patterns. For both short and long-term recaptures, movement was limited for the smallest and largest octopus, while octopus in the median (10 to 18 kg) range moved the most. In Prince William Sound, larger *E. dofleini* moved more than smaller *E. dofleini*, though only four of 50 individuals examined were greater than 15 kg (Scheel and Bisson 2012). Increased movement by median-sized *E. dofleini* might be a function of looking for mates or searching for denning habitat for spawning. In the eastern Bering Sea, the size at 50% maturity for male and female *E. dofleini* is 10.8 kg and 12.8 kg respectively (Chapter 5). In this study, increased movement rates occurred between 10 and

18 kg, suggesting that most of the movement involved mature individuals. As male *E. dofleini* can produce as many as 15 spermatophores (Chapter 5), it is likely that males can inseminate more than one female encouraging increased movement to maximize males' reproductive success (Chapter 5). Once females are inseminated, they will seek out rocky dens to lay eggs (Boyle and Rodhouse 2005), again increasing the need to move. For very small *E. dofleini*, decreased movement rates might reduce predation risk (Mather and O'Dor 1991) as large fish predators like Pacific cod and Pacific halibut are present in the area (F. Bowers, personal communication). Limited movements for very large *E. dofleini* may due to post-mating senescence of male octopus (Semmens et al. 2007).

In the eastern Bering Sea, many *E. dofleini* tended to remain in a small area over a relatively long period of time. Long-term residence in small areas has been reported for *E. dofleini* in British Columbia (Hartwick et al. 1981; Mather et al. 1985) and Prince William Sound (Scheel and Bisson 2012), *O. bimaculatus* in California (Ambrose 1982), *O. cyanea* in Hawaii (Yarnall 1969), and *O. vulgaris* in the Mediterranean Sea (Altman 1967). In British Columbia, most of the *E. dofleini* stayed in the same general location for weeks sometimes occupying the same shelter for months (Hartwick et al. 1984). Residence in a restricted area may indicate high quality of habitat, availability of food resources, or abundance of conspecifics for mating (Scheel and Bisson 2012). In this study, the high recapture rate of *E. dofleini* in the relatively small 25 km^2 study area suggests that the ecological attributes of local environment can support a large number of *E. dofleini*. Though this study was not able to determine if *E. dofleini* make seasonal onshore-offshore migrations, it appears that a large proportion of the population is not moving extensively.

Elevated temperatures associated with climate warming may have large-scale impacts on the growth and movement patterns of *E. dofleini* in the eastern Bering Sea. Increased temperatures would likely influence the sensitivity of octopus size to changes in metabolic rate (Andre at al. 2009). Predicted increases in temperature, combined with decreasing pH will decrease the ability of cephalopods to bind oxygen for transport (Seibel and Fabry 2003), therefore altering metabolic rate at the individual level. It is likely that the change in metabolic rate mirrors the change in growth for *E. dofleini* (Rigby and Sakurai 2004) and may have implications for movement. Ultimately, future environmental warming will impact the growth of octopuses, size at maturity and alter population dynamics (Andre et al. 2009). Though this study represents a new perspective for this species in the eastern Bering Sea, the study area and the scale of the mark-recapture effort are limited and further broader-scale studies are needed to determine the impacts of future environmental changes over larger regional scales.

ACKNOWLEDGEMENTS

This study was supported by the North Pacific Research Board projects 906 and 1005, Alaska Sea Grant and National Oceanic and Atmospheric Administration. I would like to thank O. Ormseth, A. Seitz, S. Tamone and A. Blanchard for reviewing this manuscript. I am also grateful to Z. Nehus, C. Stockton, K. Whittern, and T. Gibson for assistance in the field. Logistics and recapture support provided by the crew of the F/V St. Dominick.

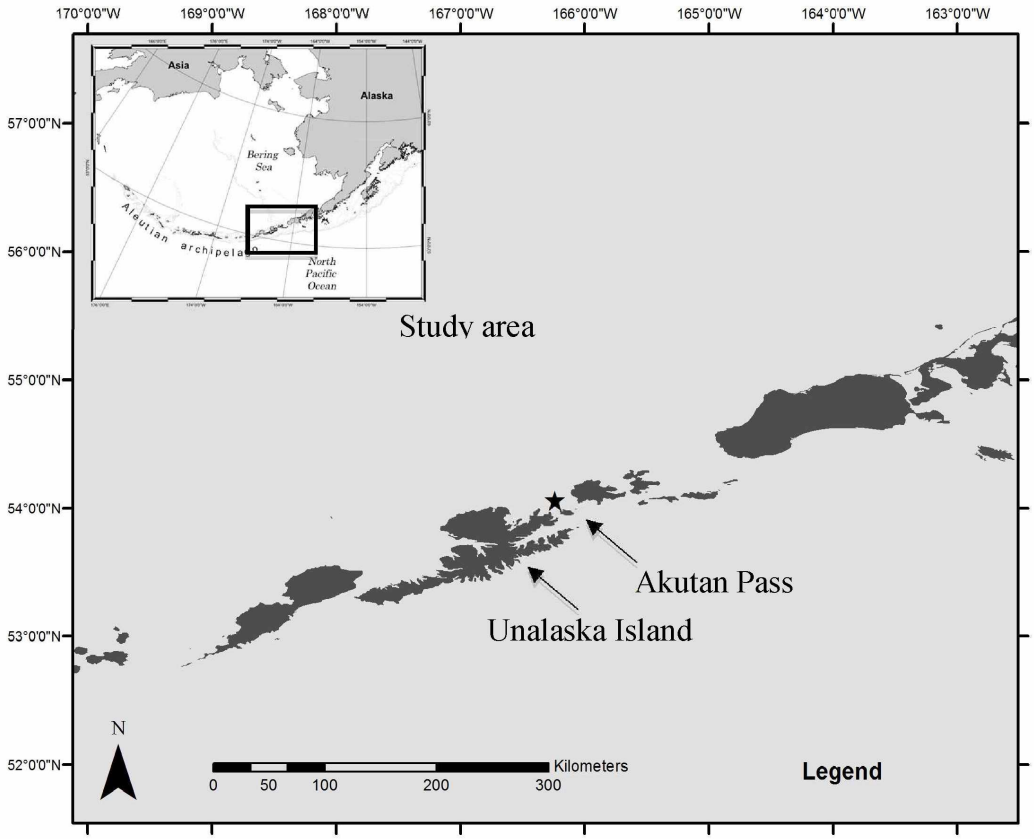


Figure 3.1. The 25 km^2 study area where *Enteroctopus dofleini* growth and movement was examined was located 20 km northeast of Unalaska Island, Alaska

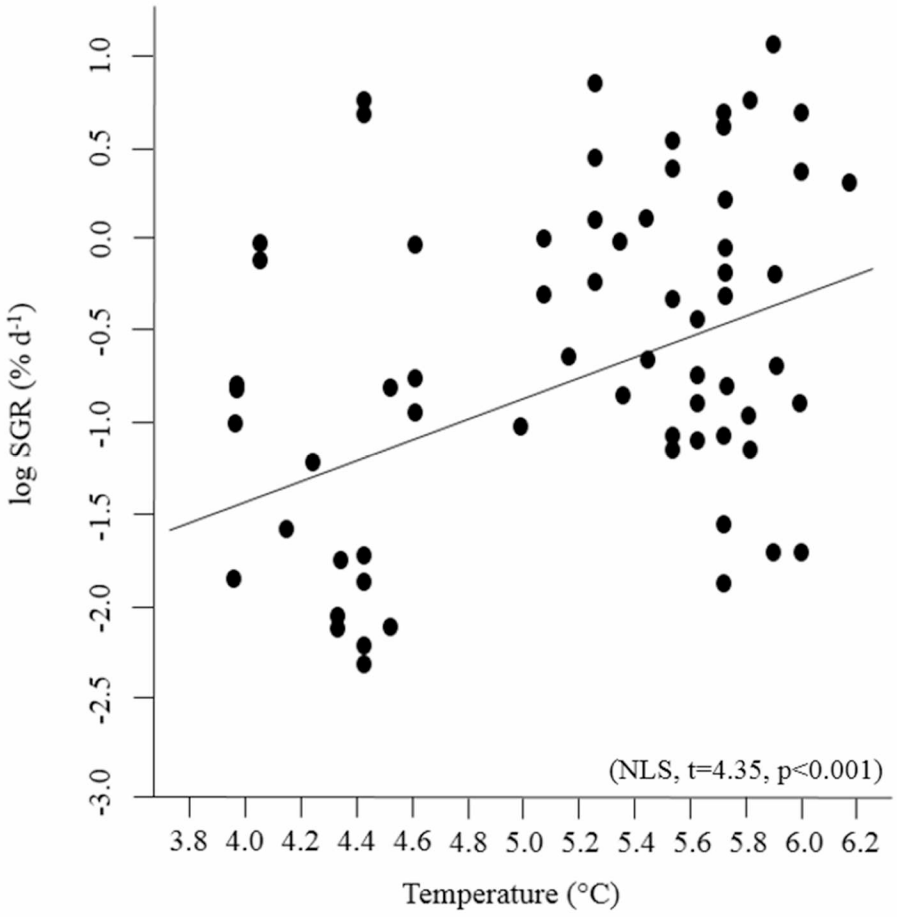


Figure 3.2. Increasing specific growth rate (SGR; % d^{-1}) with increasing temperature (°C) for short-term recaptures (<60 days) of *Enteroctopus dofleini* in the eastern Bering Sea

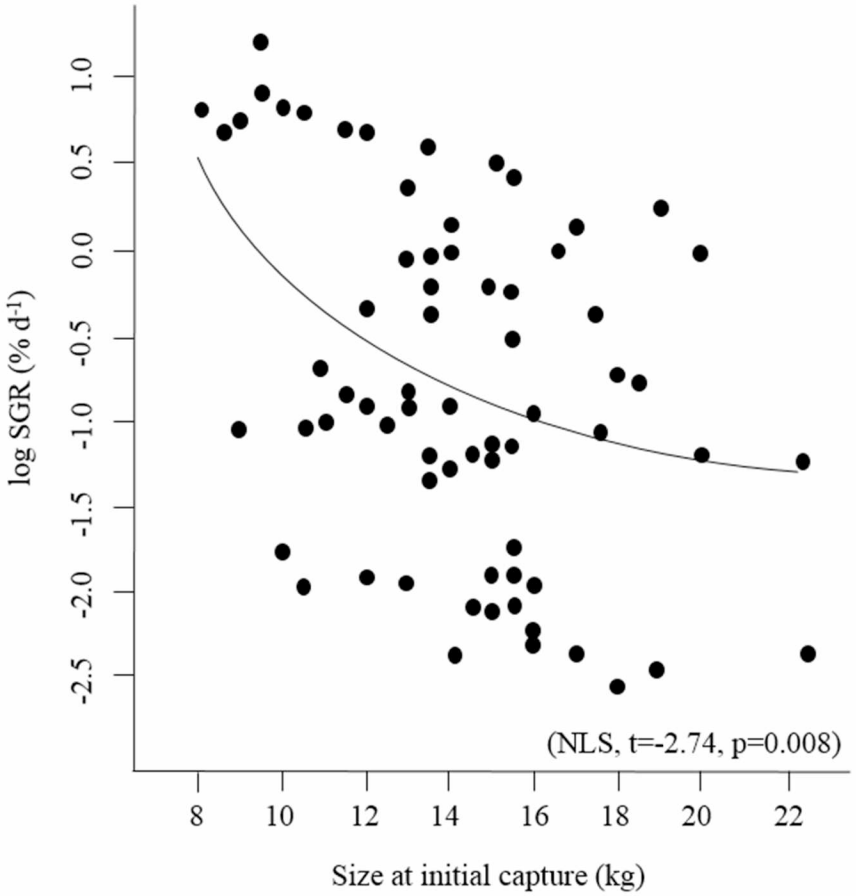


Figure 3.3. Decreasing specific growth rate (SGR; % d^{-1}) with increasing size at initial capture (kg) for short-term recaptures (<60 days) of *Enteroctopus dofleini* in the eastern Bering Sea

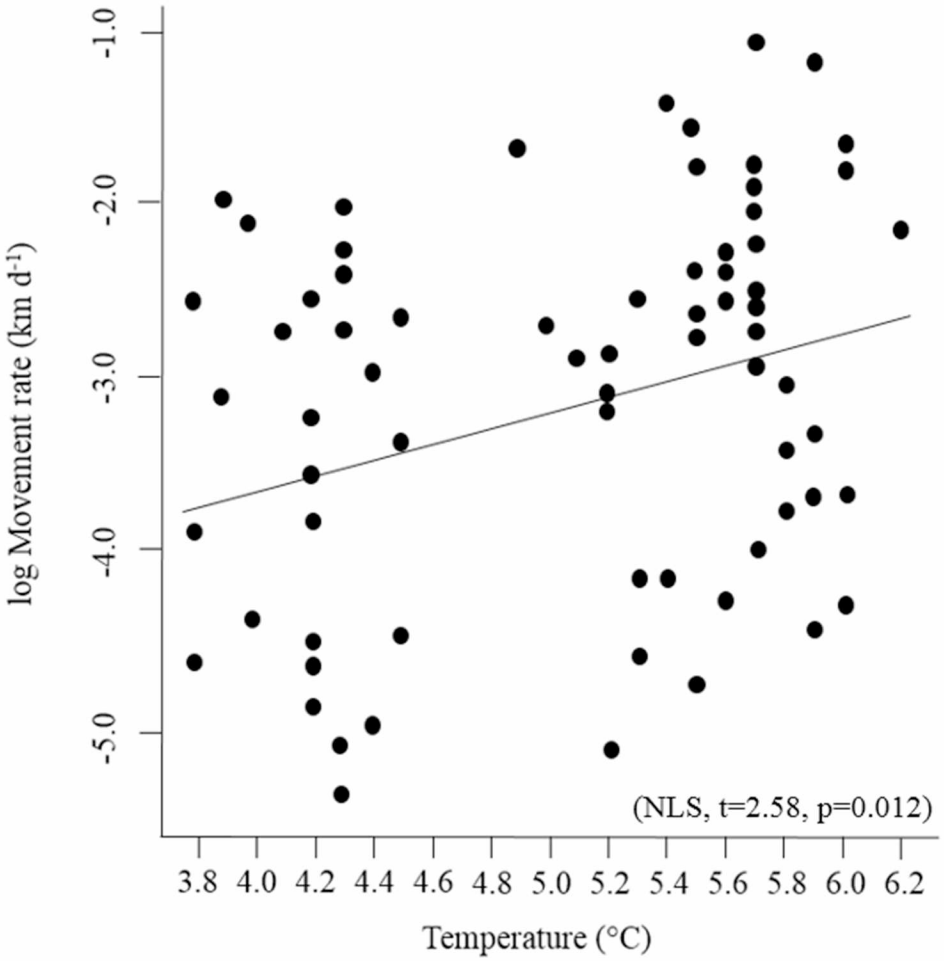


Figure 3.4. Increasing movement rate (km d^{-1}) with increasing temperature (°C) for short-term recaptures (<60 days) of *Enteroctopus dofleini* in the eastern Bering Sea

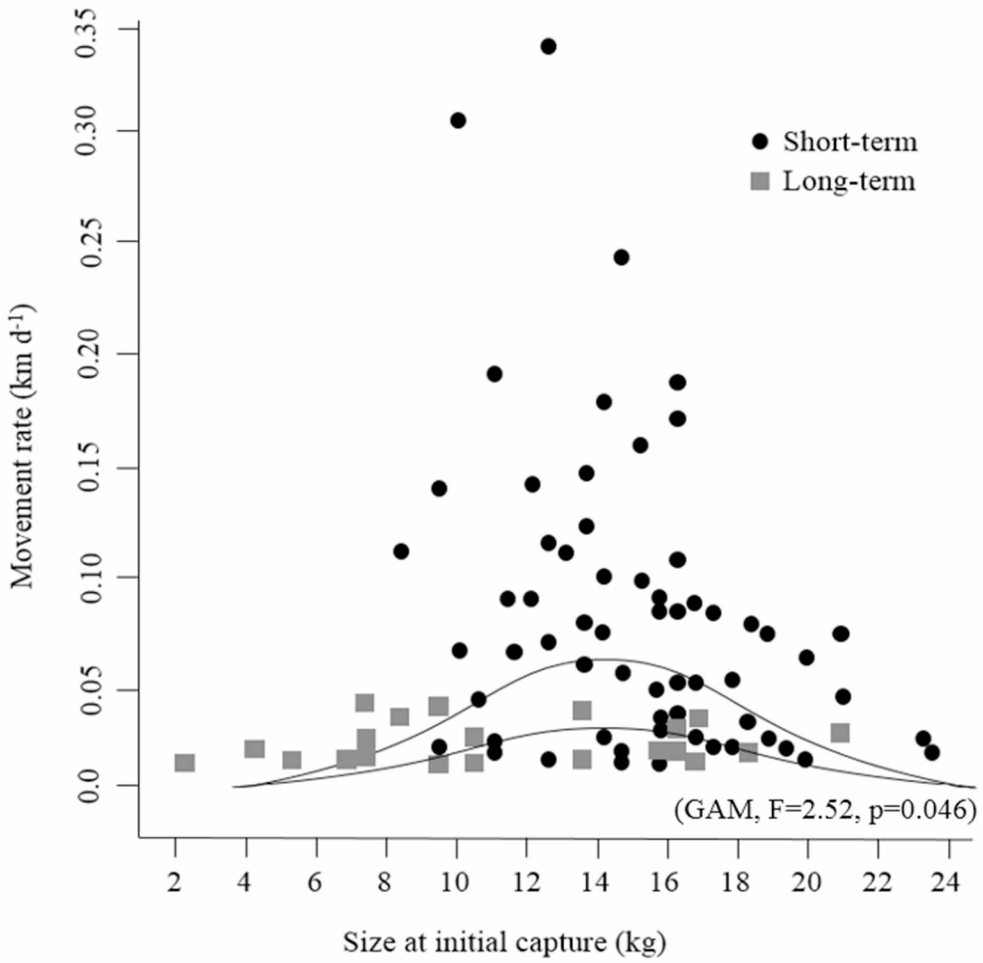


Figure 3.5. Size at initial capture (kg) and movement rate (km d^{-1}) for short-term (<60 days) and long-term (≥60 days) recaptures of *Enteroctopus dofleini* in the eastern Bering Sea

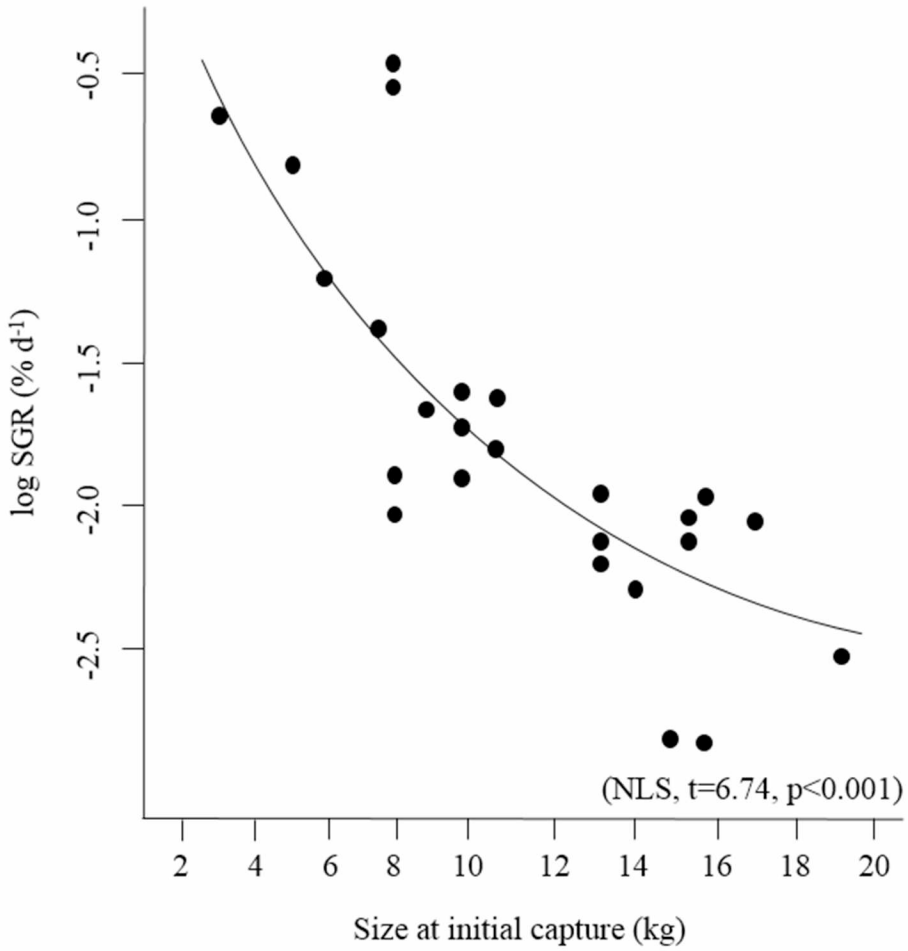


Figure 3.6. Decreasing specific growth rate (SGR; % d^{-1}) with increasing size at initial capture (kg) for long-term recaptures (≥60 days) of *Enteroctopus dofleini* in the eastern Bering Sea

Table 3.1. Description of mark-recapture operations performed on *Enteroctopus dofleini* over a three-year period in the eastern Bering Sea

	autumn 2009	*winter 2010*	*autumn 2010*	*winter 2011*	*autumn 2011*	*total*
Months sampled	October November	February March	September October	January February	September October	
Mean temperature (°C ± SE)	5.62 ± 0.02	3.93 ± 0.02	5.23 ± 0.39	4.28 ± 0.02	5.52 ± 0.01	
Days of tagging	10	5	10	7	9	41
Days of recapture	15	46	16	77	29	183
Octopus tagged	244	159	452	286	573	1,714
Mean weight (kg ± SE)	13.1 ± 0.3	12.2 ± 1.0	14.8 ± 0.2	13.9 ± 0.3	14.6 ± 0.1	
Octopus recaptured	17	19	57	43	110	246
Sex ratio (M:F)	2.7:1.0	1.9:1.0	1.8:1.0	3.1:1.0	2.2:1.0	
Number of same-season recaptures	17	11	48	37	108	221

Table 3.2. Size at initial capture and specific growth rate (SGR) for male and female *Enteroctopus dofleini* recaptured in less than 60 days after release (short-term) during autumn and winter in the eastern Bering Sea. Of the 214 first time recaptures, only 71 were analyzed for short-term analyses. Size at initial capture and SGR are reported as (mean ± SE)

	Females			Males			Total	
	N	Size at initial capture (kg)	SGR (% d^{-1})	N	Size at initial capture (kg)	SGR (% d^{-1})	N	SGR (% d^{-1})
Autumn	10	13.0 ±0.8	1.3±0.03	36	14.8±0.5	0.9±0.1	46	0.957±0.12
Winter	3	10.3±0.9	0.2±0.01	22	14.8±0.7	0.3±0.1	25	0.297±0.06

LITERATURE CITED

Altman JS. 1967. The behaviour of *Octopus vulgaris* in its natural habitat: a pilot study. Underwater Assoc Rprt 1966-1967:77-83

Ambrose R. 1982. Shelter utilization by the molluscan Cephalopod *Octopus bimaculatus*. Mar Ecol Prog Ser 7:67-73

Andre JEP, Grist M, Semmens JM, Pecl GT, Segawa S. 2009. Effects of temperature on energetics and the growth pattern of benthic octopuses. Mar Ecol Prog Ser 374:167-179

Barry PD, Brewer RS, Browning J, Grund J, Scheel D, Tallmon D, Tamone S. 2007. Investigation of tagging methods and tracking for Giant Pacific Octopus (*Enteroctopus dofleini*) in Southcentral Alaska. AFDF Final Report. 40p

Barry PD, Tamone SL, Tallmon DA. 2011. A comparison of tagging methodology of North Pacific giant octopus *Enteroctopus dofleini*. Fish Res 109:370-372

Borer KT, Lane CE. 1971. Oxygen requirements of *Octopus briareus* (Robson) at different temperatures and oxygen concentrations. J Exp Mar Biol Ecol 7:263-269

Boyle PR, Knobloch D. 1982. On growth of the octopus *Eledone cirrhosa*. J Mar Biol Assoc U.K. 62(2):277-296

Boyle PR, Rodhouse P. 2005. Cephalopods: Ecology and Fisheries. Blackwell Publishers

Castro BG, Lee PG. 1994. The effects of semi-purified diets on growth and condition of *Sepia officinalis*. Comp Biochem Physiol 109A:1007-1016

Conrath CL, Conners ME. 2014. Aspects of the reproductive biology of the North Pacific giant octopus (*Enteroctopus dofleini*) in the Gulf of Alaska. Fish Bull 112:253-260

Cortez T, Gonzalez AF, Guerra A. 1999. Growth of *Octopus mimus* (Cephalopoda, Octopodidae) in wild populations. Fish Res 42:31-39

Domain F, Jouffre D, Caveriviere A. 2000. Growth of *Octopus vulgaris* from tagging in Senegalese waters. J Mar Biol Assoc U.K. 80:699-705

Doubleday ZA, Semmens JA. 2010. Quantification of the age-pigment lipofuscin in known-age octopus (*Octopus pallidus*): A potential tool for age determination. J Exp Mar Biol Ecol 397:8-12

Forsythe JW. 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. In: Recent Advances in Cephalopod Fisheries Biology, pp. 133 – 144. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai, University Press, Tokyo

Gillespie GE, Parker G, Morrison J. 1998. A Review of Octopus Fisheries Biology and British Columbia Octopus Fisheries. Fisheries and Oceans Canada, issn 1480-4883

Hamazaki H, Fukunaga K, Yoshida Y, Maruyama K. 1991. Effects of marine microalgae *Nannochloropsis* sp. on survival and growth on rearing pelagic paralarvae of *Octopus*

vulgaris, and results of mass culture in the tank of 20 metric tons. Saibai-giken 19:75–84

Hartwick EB, Tulloch L, MacDonald S. 1981. Feeding and growth of *Octopus dofleini*. Veliger 24:129-138

Hartwick EB, Ambrose RF, Robinson SMC. 1984. Dynamics of shallow-water populations of *Octopus dofleini*. Mar Biol 82:65-72

Hartwick EB, Robinson SMC, Ambrose RF, Trotter D, Walsh M. 1988. Inshore-offshore comparison of *Octopus dofleini* with special reference to abundance, growth and physical condition during winter. Malacologia 29:57-68

Hernandez-Lopez JL, Castro-Hernandez JI, Hernandez-Garcia V. 2001. Age determined from daily deposition of concentric rings on common octopus (*Octopus vulgaris*) beaks. Fish Bull 99:697-684

Iribarne OO. 1991. Life history and distribution of the small south-western Atlantic octopus, *Octopus tehuelchus*. J Zool 223:549-565

Jabeur C, Nouira T, Khoufi W, Saidaine-Mosbahi D, Ezzeddine-Najai S. 2012. Age and growth of *Octopus vulgaris* Cuvier, 1797, along the east coast of Tunisia, J Shell Res 31:119-124

Johnson TL. 2003. The Bering Sea and Aleutian Islands – Region of Wonders. Alaska Sea Grant, University of Alaska Fairbanks

Jorgensen EM. 2009. Field guide to Squids and Octopods of the Eastern North Pacific and Bering Sea. Alaska Sea Grant College Program, University of Alaska Fairbanks

Kanamaru S, Yamashita Y. 1966. The results of tagging studies of Mizudako which were carried out from 1960-1965 in the northern part of the Japan Sea. Report of the Hokkaido Marine Research Center

Katsanevakis S, Verriopoulos G. 2004. Abundance of *Octopus vulgaris* on soft sediment. Sci Mar 68:553-560

Kaufmann KW. 1981. Fitting and using growth curves. Oecologica 49:293-299

Mangold KM, Boletsky SV. 1973. New data on reproductive biology and growth of *Octopus vulgaris*. Mar Biol 19:7-12

Mather JA, O'Dor RK. 1991. Foraging strategies and predation risk shape the natural history of Juvenile *Octopus vulgaris*. Bull Mar Sci 49(1-2):256-269

Mather JA, Resler S, Cosgrove J. 1985. Activity and movement pattern of *Octopus dofleini*. Mar Behav Physiol 11:301-314

Mottet MG. 1975. A technical report on the fishery biology of *Octopus dofleini*. Washington Department of Fisheries, Tech Rep. No 16, 38p

Perez MC, Lopez DA, Aguila K, Gonzalez ML. 2006. Feeding and growth in captivity of the octopus *Enteroctopus megalocyathus* Gould, 1852. Aquac Res 37:550-555

Pickford GE. 1964. *Octopus dofleini* (Wülker). Bull., Peabody Mus Nat Hist 19:5-70

Pierce GJ, Key LN, Boyle PR, Siegert KJ, Goncalves JM, Porteiro FM, Martins HR. 1999. RNA concentration and the RNA to protein ration in cephalopod tissues: sources of variation and relationship with growth rate. J Exp Mar Biol Ecol 237:185-201

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.Rproject.org, accessed 10 February 2015

Rigby PR, Sakurai Y. 2004. Temperature and feeding related growth efficiency of immature octopuses *Enteroctopus dofleini*. Suisanzoshoku 52(1):29-36

Robinson SMC, Hartwick EB. 1986. Analysis of growth based on tag-recapture of the giant Pacific octopus (*Octopus dofleini martini*). J Zool 209:559-572

Robinson SMC. 1983. Growth of the giant Pacific octopus (*Octopus dofleini martini*) on the west coast of British Columbia. MS thesis, Simon Fraser University, Canada

Sato K, Yorita T. 1999. Fishing trends and migration of the North Pacific giant octopus dofleini in Tsugaru Straits. Science Report Hokkaido Fisheries Experimental Station 56, 119-124

Scheel D. 2002. Characteristics of habitats used by *Enteroctopus dofleini* in Prince William Sound and Cook Inlet, Alaska. Marine Ecology 23(3):185-206.

Scheel D, Bisson L. 2012. Movement patterns of giant Pacific octopuses, *Enteroctopus dofleini* (Wülker, 1910). J Exp Mar Biol Ecol 416-417:21-31.

Seibel BA, Fabry VJ. 2003. Marine biotic response in elevated carbon dioxide. In: Hannah L, Lovejoy T (eds) Climate change and biodiversity: synergistic impacts, Vol 4. Center of Applied Biodiversity Science, Conservation International, Washington, DC, p 59-67

Semmens JM, Pecl GT, Villanueva R, Jouffre D, Sobrino I, Wood JB, Rigby PR. 2004. Understanding octopus growth: patterns, variability and physiology. Mar Fresh Res 55:367-377

Semmens JM, Pecl GT, Gillanders BM, Waluda CM, Shea EK, Jouffre D, Ichii T, Zumholz K, Katugin ON, Leporati SC, et al. 2007. Approaches to resolving cephalopod movement and migration patterns. Rev Fish Biol Fisheries 17:401-423

Storero LP, Ocampo-Reinaldo M, González RA, Narvarte MA. 2010. Growth and life span of the small octopus *Octopus tehuelchus* in San Matías Gulf (Patagonia): three decades of study. Mar Biol 157:555–564

Van Heukelem WF. 1976. Growth, bioenergetics and life-span of *Octopus cyanea* and *Octopus maya*. PhD dissertation, University of Hawai'i, Honolulu

Von Bertalanffy L. 1950. An Outline of General System Theory. Brit J Phil Sci 1(2):134-165

Wells MJ, Wells J. 1970. Observations of the feeding, growth rate and habits of newly settled *Octopus cyanea*. J Zool 161(1):65-74

Wood JB, O'Dor RK. 2000. Do larger cephalopods live longer? Effects of temperature on phylogeny on interspecific comparisons of age and size at maturity. Mar Biol 136:91-99

Yarnall JL. 1969. Aspects of the behavior of *Octopus cyanea* (Gray). Anim Behav 17(4):747-754

CHAPTER FOUR

Estimates of abundance and survival of the North Pacific giant octopus (*Enteroctopus dofleini*) in the eastern Bering Sea[1]

ABSTRACT: Though the North Pacific giant octopus (*Enteroctopus dofleini*) represents a large incidental commercial catch in Alaska, little is known about the population attributes of this species and therefore management capability is also limited. I used Cormack-Jolly-Seber models to estimate the survival and population size for *E. dofleini* in the eastern Bering Sea. Models were constructed using mark-recapture data from a tagging effort performed from 2009 to 2011. Over the course of this study, 1,714 *E. dofleini* were tagged and 246 were recaptured. The population estimate for *E. dofleini* in the 25 km^2 study area was 3,180 octopus ± 2658 SE and the estimated annual survival rate was 3.33% ± 2.69 SE. Though the present study represents a small portion of the eastern Bering Sea, the estimates presented here show that octopus abundance in certain portions the Bering Sea/Aleutian Islands is significant, and federal management catch estimates for octopus are too conservative or inappropriate.

[1]Brewer RS, Ormseth O, Norcross BL. In prep. Estimates of abundance and survival of the North Pacific giant octopus (*Enteroctopus dofleini*) in the eastern Bering Sea. Fish Res

INTRODUCTION

The North Pacific giant octopus (*Enteroctopus dofleini*) is an important commercial resource in Japan, a recreational resource in British Columbia, and a large incidental commercial catch in Alaska. In Japan, *E. dofleini* represent a large portion of the annual octopus catch, which can exceed 100,000 mt (Boyle and Rodhouse 2005). In British Columbia, small trap and dive fisheries for *E. dofleini* have historically caught less than 217 mt per year (Fisheries and Oceans Canada 2005). In Alaska, the incidental catch of octopus varies between 50 and 400 mt per year, with a maximum catch of 534 mt in 2011 (Conners et al. 2014). In the United States, there has never been a directed fishery for *E. dofleini* in federal waters, although there has been some interest in this resource by export markets (Paust 1988).

In Alaska, *E. dofleini* is incidentally caught in state and federally managed bottom-trawl, longline and pot fisheries (Conners et al. 2014). Management of *E. dofleini* in Alaska has been problematic, partly due to inappropriate survey methods (Conners et al. 2014). Though trawl survey data yield the most reliable biomass estimates for most federally managed fish and invertebrates, it is unlikely that these surveys are sufficient to represent the population of *E. dofleini* that are subject to harvest (Conners et al. 2014).

In 2011, all eight species of octopus found in the Bering Sea/ Aleutian Islands (BSAI) were grouped into an "octopus complex" and managed using the maximum historical incidental catch, though *E. dofleini* make up 80% of the Bering Sea shelf octopus biomass (Conners et al. 2012). In October of 2011, the octopus catch exceeded the over fishing limit (OFL) of 528 mt, and all fishing using pot gear in the BSAI was closed. As a result of the closure, the remaining 1,615 mt in quota for Pacific cod (*Gadus macrocephalus*) were not caught, resulting in a lost opportunity cost of approximately $1 million dollars (NMFS 2012). In 2012, federal fisheries

managers increased the OFL for octopus to 3,452 mt based upon a consumption estimate of octopus by Pacific cod (*Gadus macrocephalus*; Conners et al. 2014). The consumption estimate is considered conservative, as Pacific cod is only one of many species that eat octopus in the Bering Sea. Fisheries managers suggest that octopus management should be based upon more rigorous biomass and mortality estimates using tag and recapture studies (Conners et al. 2014), like those performed as another part of this research (Chapter 2).

In this study, I used a relatively new tagging technology that allowed me to estimate important population parameters using a mark-recapture study. This three-year study estimated the abundance and survival of *E. dofleini* in a 25 km^2 area of the eastern Bering Sea (EBS). I was able to track octopus over periods of >1 year, and to estimate survival and abundance for this data-poor species. My specific objectives were to 1) identify the factors that influence survival and capture probabilities of *E. dofleini*, 2) estimate survival rates and capture probabilities, and 3) estimate density, abundance and biomass. The present study was performed in the region that has accounted for the greatest incidental catch of *E. dofleini* in the EBS, and the results are therefore especially pertinent to the management and conservation of this population.

METHODS

Mark-recapture Operations

Mark-recapture operations were performed 20 km northeast of Unalaska Island, AK from October 2009 to November 2011 (center of study area 54° 04'N, 166° 25'W; Fig. 4.1; Table 4.1). The study area was approximately 25 km^2, and the substrate was composed of a mix of sand, gravel and rock (personal observations), with sample depths ranging from 75 to 225 m. The study area was approximately 20 km northwest of Akutan Pass, a narrow shallow channel that allows the transfer of water between the Gulf of Alaska and the Bering Sea. Mixing in

Akutan Pass creates a productive ecosystem that supports a diverse array of marine organisms and productive commercial fisheries for several species, including Pacific cod and Pacific halibut (*Hippoglossus stenolepis*; Johnson 2003).

Octopus tagging was conducted on the F/V St. Dominick during normal commercial fishing operations for Pacific cod. Octopus were captured opportunistically in standard 2.5 x 2.5 x 0.9 m groundfish pots with two openings (20.3 x 91.4 cm) baited with Pacific herring (*Clupea pallasii*). Pots were fished at all hours of the day and night and soak times varied from 12 to 72 hours depending upon the weather.

Octopus were tagged in five seasonal periods occurring in alternating autumns (September–October) and winters (January–March) beginning in autumn 2009 and ending in autumn 2011 (Table 4.1). Tagging periods lasted 5 to 10 days and one person performed all tagging operations to ensure standardization of protocols. Captured octopus missing more than one arm or found with tears in the mantle were not used in this study. Octopus missing only one arm or with minor damage to skin were still used in this study and the injuries were documented.

Captured octopus were sexed, measured and marked with Northwest Marine Technologies Visible Implant Elastomers (VIEs; Chapter 2). Octopus were sexed by observing the hectocotylized 3rd right arm of males and the absence of a hectocotylized 3rd right arm for females. Octopus were blotted with absorbent towels to remove excess water and wet weight was measured to the nearest 0.5 kg using a hanging spring scale. Each day scales were calibrated to account for changing ocean conditions. Individual octopus were given a six color VIE sequence on the ventral portion of the mantle as described in Chapter 2, and sex, weight (kg), and color code were recorded for each individual. Geographic location, day, time, and depth (m) were recorded for each retrieved pot.

Recaptures of octopus occurred during the same seasons as the tagging activities (Table 4.1). Recapture periods included all of the tagging days, as many octopus were recaptured shortly after tagging. Typically, tagging occurred in the early portion of the charters and recaptures occurred later spanning 15 to 77 days. Identification and measurement of recaptured octopus were performed by three trained individuals. Recaptured octopus were evaluated for signs of external damage and VIEs were evaluated for readability and integrity. Recaptured octopus were sexed, weighed and re-released in the same manner as described above for the initial tagging, and pot retrieval data were recorded as previously described.

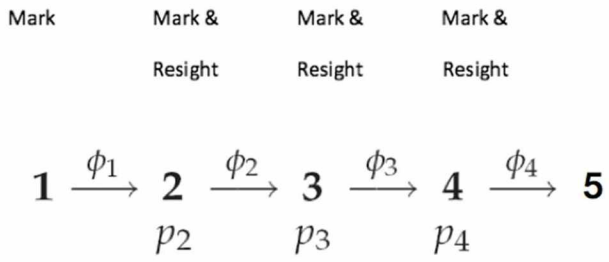
To evaluate the potential for tag-induced mortality, the first octopus captured each day of the tagging operations was tagged and kept in a fish tote with circulating seawater for 12 hours. At the end of the 12-hour period, the octopus' condition was evaluated based upon its color and activity using a three-stage viability coding (Excellent, Poor, Dead) as described by Conners et al. (2012).

Mark-Recapture Analysis

Estimation of *E. dofleini* survival and population size in the Bering Sea involved several steps. The analysis was based on the Cormack-Jolly-Seber (CJS) tagging model, which allows estimation of survival rates and inclusion of the most appropriate covariates such as individual size, as the most appropriate model for this analysis (see Lebreton et al. 1992). I used CJS models for open populations following the parameterization of Amstrup et al. (2005) that allowed for the incorporation of external covariates into linear-logistic equations for probability of capture and probability of survival. The estimates from the CJS models were then used with

the Horvitz-Thompson (HT) estimator (McDonald and Amstrup 2001; Amstrup et al. 2005) to produce estimates of abundance for the study area.

The CJS model was used as it is the most appropriate to incorporate covariates and meet project objectives. Similar to the original Jolly-Seber (JS) model, the CJS models allow for the estimation of survival (φ), capture probability (p), population size (N) and the number of new individuals entering the population (B; Lebreton et al. 1992). While population size can be estimated using J-S models, these models are known to have substantial bias in the estimation of population size due to individual heterogeneity (White et al. 1982). The CJS model is more conservative than JS models and allows year-specific estimates of φ and p, and only CJS models can estimate survival (Lebreton et al. 1992). The CJS models are based upon Pollock's robust design to incorporate closed population models for short secondary sampling time periods and open population models for longer primary sampling periods (Amstrup et al. 2005). The CJS models are conditional on the first capture and estimate the probabilities of survival (φ) and capture (p) which are most likely to explain the observed capture history (Lebreton et al. 1992).



The use of CJS models requires that several assumptions are addressed to ensure accuracy and appropriateness of model selection. For this study, I assumed the population size changed during the course of the study (Pollock 1982). I also assumed that marked octopus had an equal probability of capture due to the heterogeneity associated with sex and body weight. The time frames for this study were short and the assumption associated with tag fading and tag-

induced mortality was met by using multiple colored tags for each octopus and tag-induced mortality studies (Chapter 2). To standardize tagging and minimize improperly read or missed tags, a single person tagged octopus, and tag recoveries were identified by one of three trained individuals. I assumed emigration from the study area was permanent as a result of reproductive activities leading to death, as *E. dofleini* may maintain long-term den site fidelity for periods exceeding a year (Chapter 2). As *E. dofleini* are solitary organisms, I assumed that octopus were randomly sampled from the population and their fates were independent of other conspecifics.

To explore possible predictors of survival and capture probability, I used a logistic-link function for CJS models to estimate φ and p as linear functions of external covariates (McDonald and Amstrup 2001). This approach used φ and p as response variables and sex, weight class, depth, temperature, season, number of days of capture effort (days), number of pots fished during capture time (pots), and time as explanatory variables. Individuals were assigned to four weight classes using 25th percentiles of size data: <12 kg, 12 to <14 kg, 14 to <16 kg, and ≥16 kg. The R-language software (R Development Core Team 2010) and R package mra (T. McDonald, http://cran.cnr.berkeley.edu/web/packages/ mra/index) were used to implement a general regression approach (Amstrup et al. 2005), a parameterization of the CJS likelihood that fits the same models and produces the same parameter estimates as other software (eg. Program MARK; Cooch and White 2005). Sex was randomly assigned to 60 *E. dofleini* that could not be sexed in the field using ratios consistent with initial capture.

The preferred model was chosen in three steps: (1) all possible combinations of capture probability covariates were fitted in conjunction with a constant survival model; (2) all possible combinations of survival probability covariates were fitted in conjunction with a constant capture model; and (3) all combinations of the top four models from steps (1) and (2), plus the intercept-

only model, were fitted. The best models at the end of each step were chosen by using the Akaike Information Criterion (AIC) to identify the lowest AIC among the 25 (5 x 5) models fitted during step (3). Models that did not converge were excluded. I used a bootstrap procedure with replacement to estimate confidence intervals of model coefficients. Individual octopus were resampled 500 times and the model was refit with each of the 500 data sets. The coefficients from each fit formed the bootstrap distribution for each coefficient. The 95% confidence limits were the 0.025^{th} and 0.975^{th} percentiles of the bootstrap distribution (Manly 1997). Statistical analyses of data were conducted in R (R Development Core Team 2010), with significance levels of alpha = 0.05, and means reported with ± SE unless otherwise noted.

Population estimates were calculated using estimates of capture probabilities derived from the CJS models and the Horvitz-Thompson (HT) estimator (McDonald and Amstrup 2001; Amstrup et al. 2005). The HT estimator was needed because open population abundance cannot be estimated by CJS models while incorporating external covariates (McDonald and Amstrup 2001). The HT estimator tracks population size even when the open population experiences relatively large and rapid changes (McDonald and Amstrup 2001). The Horvitz-Thompson (HT) estimator is equal to the inverse of the capture probability summed over all animals, i.e., the number of animals captured in a given time period divided by the capture probability:

$$\hat{N}_j = \sum_{i=1}^{nj} \frac{I_{ij}}{\hat{p}_{ij}}$$

where N_j is the abundance estimate, I_{ij} equals 1 if animal i was caught at time j, and p_{ij} is the capture probability for animal i at time j. The HT estimator makes inferences about the population that has non-zero capture probability in the particular season for which it was constructed. Application of the HT estimator assumes that an unequal probability sample of *E. dofleini* was obtained during each sampling occasion, and the capture probability model is

correct for all *E. dofleini* captured one or more times. The variance of N was obtained using the Taylor series approximation (Amstrup et al. 2005):

$$\mathrm{var}(\hat{N}_j) = \sum_{i=1}^{n} \frac{h_{ij}(1-\hat{p}_{ij})}{\hat{p}^2{}_{ij}} \left[1 + \frac{3\,\mathrm{var}(\hat{p}_{ij})}{\hat{p}^2{}_{ij}} + \frac{\left[\mathrm{var}(\hat{p}_{ij})\right]^2}{\hat{p}^4{}_{ij}} \right] + \sum_{i=1}^{n} \sum_{i'=1}^{n} \frac{h_{ij} h_{i'j}\,\mathrm{cov}(\hat{p}_{ij}, \hat{p}_{i'j})}{\hat{p}^2{}_{ij}\,\hat{p}^2{}_{i'j}}$$

where h_{ij} is the jth entry in the capture history for animal I, n is the number of animals, var ($\hat{p}_{ij}$) is the estimated capture probability of the ith animal at time j, cov($\hat{p}_{ij}$, $\hat{p}_{i'j}$) is the covariance between animal i and i' during time j (Amstrup et al. 2005). To obtain a single estimate for the population size over the length of this study, the estimates for the three open periods (autumn 2009 to winter 2010, winter 2010 to autumn 2010, and autumn 2010 to winter 2011) were averaged and the confidence interval for this estimate was obtained with a bootstrap procedure.

To determine catch limits in federal fisheries, estimates of biomass and mortality allow fisheries biologists to set overfishing limits and acceptable biological catch rates. To estimate the biomass of *E. dofleini* in federal management areas 509, 517 and 519 (Fig. 4.1), where most of the incidental catch of octopus occurs in the EBS, I expanded the study-area estimate using catch information from the Alaska Fisheries Science Center (AFSC) observer program. The AFSC stratifies observer data in the BSAI using rectangular 400 km^2 strata (the "observer block"). The catch per unit effort (CPUE; # of octopus/100 pots) observed in the present study (24 octopus/100 pots) was very similar to the 20-year average CPUE in the AFSC observer block that contained the study area (23 octopus/100 pots). Under the assumption that CPUE is consistent throughout the study-area block (block 0), the abundance estimate of the 25 km^2 study area was expanded to the entire block ($N_{\text{block 0}} = N_{\text{study area}} * 16$). An abundance estimate for each block in areas 509, 517, and 519 was calculated as the block-0 abundance estimate multiplied by

the ratio of the block-specific CPUE to the block-0 CPUE; the estimates from each block were then summed to give an overall estimate for the three areas, resulting in the following equation:

$$N_{overall} = \sum_{i=1}^{n} N_{block\ 0}\left(\frac{CPUE_{block\ i}}{CPUE_{block\ 0}}\right)$$

where n is the total number of blocks. Biomass was estimated by multiplying $N_{overall}$ by the mean weight of octopus in the study. To estimate mortality (M) of *E. dofleini* I used a logarithmic conversion of survival (S) where M = -ln (S). I estimated both monthly and annual mortality for immature and mature male and female *E. dofleini*.

RESULTS

General

From autumn 2009 to autumn 2011, groundfish pots were deployed 15,491 times during 256 days of tag and recapture operations. Mean soak time for pots was approximately 18.2 hours ± 3.2 and the mean number of octopus captured in 100 pots was 24 ± 1 SE. A total of 1,714 *Enteroctopus dofleini* was captured and tagged with VIEs and released. The size of *E. dofleini* at initial capture ranged between 0.5 kg and 30.0 kg with a mean of 14.1 kg ± 0.1 (Fig. 4.2). Males tended to be larger than females with a mean size of 14.6 kg ± 0.1 and 13.0 kg ± 0.2 respectively. Of the 1,714 *E. dofleini* captured and tagged, 67% were male, 30% were female and 3% could not be determined. Over the three-year study period, only 17 *E. dofleini* were excluded from tagging operations due to missing arms or damaged mantle tissues.

Recapture efforts resulted in 246 recaptures, a 14% recapture rate. Of the 246 recaptures, 186 were recaptured once, 24 were recaptured twice and 4 were recaptured three times. Only

three of the recaptured *E. dofleini* had damage to their mantle tissues or were missing arms since their initial capture. All recaptured octopus showed color and mobility consistent with a rating of Excellent according to the coding described by Conners et al. (2012). The mean size of *E. dofleini* recaptured only once was 14.5 kg ± 0.2 (n = 214); 83% were male, 16% were female and 1% could not be determined. The mean size of *E. dofleini* captured more than once was 15.1 kg ± 0.6 (n = 28); 85% were male, 11% were female and 3% could not be determined. *E. dofleini* were recaptured from 1 to 374 days after tagging. One hundred eighty three were recaptured in the same season with a mean time at liberty of 10.5 days ± 1.0, and 31 were recaptured in a subsequent sampling season with a mean time at liberty of 179.2 days ± 21.4. The longest time between tag and recapture for this study was 374 days at liberty for a male octopus that grew from 6.5 kg to 16.5 kg. None of the tags observed showed any signs of fading and none of the recaptured octopus were missing any of the VIEs as part of individual marking sequence (Table 4.1).

Model selection and parameter estimates

Model selection for the combination of probability of capture and survival yielded models with several significant covariates (Table 4.2). The final capture model included pots pulled, days fished and octopus weight (Table 4.3). The larger number of pots pulled and increased number of days fished resulted in a greater probability of capture, while increased octopus weight decreased probability of capture (Table 4.4). The final survival model included sex and weight (Table 4.3). For females and males, mean annual survival was 0.45% ± 0.55 and 6.20% ± 4.60 respectively with an overall survival of 3.33% ± 2.70. For each sex, survival

decreased with increasing weight (Fig. 4.3), and survival for immature *E. dofleini* of both sexes was higher than survival for mature *E. dofleini* (Table 4.5).

Mortality, abundance and biomass estimates

Estimates of mortality, abundance and biomass were calculated using the results of CJS models. Annual mortality for female and male *E. dofleini* was $M = 5.40$ and $M = 2.78$ respectively with a mean of $M = 3.40$. The abundance estimates in the 25 km^2 study area ranged from 2,789 octopus ± 1,659 to 3,755 octopus ± 2,996 with a mean of 3,180 octopus ± 2,658 (Table 4.6), or a density of 127 individuals km^{-2}. Extending the octopus density to the larger 400 km^2 observer block that contained the study area resulted in an abundance of 50,880 octopus. Using the federal observer data, the estimate for octopus abundance in the 3,500 km^2 area consisting of statistical areas 509, 517, and 519 was 1.47 million octopus. Considering mean size of octopus captured in this study was 14.1 kg, biomass was 44.8 mt in the study area, 717 mt in the 400-km^2 observer block containing the study area, and 20,697 mt in statistical areas 509, 517 and 519 (Fig. 4.4).

DISCUSSION

This study presents important new information for understanding the *Enteroctopus dofleini* population in the EBS. This is the first empirical estimate of octopus survival and mortality in the EBS, and both survival and mortality were dependent on octopus size and sex. Octopus size and fishing effort were predictors of capture probability and abundance of *E. dofleini* in the 25-km^2 study area. Using federal observer data, I presented estimates for the

biomass of *E. dofleini* in three neighboring regions of the EBS where most of the incidental catch of the species occurs. Though this study is limited in scope and scale, the proven protocols provided here may help guide future research in the EBS.

The positive effect of increased effort on capture probability is likely due to a combination of small study-area size and high octopus residence times. In the EBS, *E. dofleini* show limited movement patterns and residence times of up to a year (Chapter 3). Therefore, it is likely that increased effort in the study area results in increased recaptures of these individuals with limited mobility. Other attempts at using VIEs with *E. dofleini* had low recapture numbers due to limited pot pulls, a small number of octopus tagged and sampling in a large spatial area (Bush 2006; Barry et al. 2011).

Larger individuals likely have a higher capture probability than smaller individuals because of size-specific behaviors, including frequency and extent of movement, and ability to escape gear (Conners et al. 2014). In this study, the majority of the octopus captured were large and likely mature. Similarly, data from federal groundfish observers showed that the size distribution of octopus caught is gear dependent, with commercial pot gear catching primarily large individuals, while long-line and bottom trawls capturing smaller individuals (Conners et al. 2014). It is possible that pot gear is more selective for larger, more aggressive individuals that respond more strongly to bait, and that smaller individuals have a better ability to escape from the narrow opening of commercial pots while they are being retrieved (Conners et al. 2014). In Alaska, larger and potentially mature *E. dofleini*, move farther than smaller individuals (Scheel and Bisson 2012; Chapter 3). This is probably a function of searching for mates or travelling to find spawning or denning habitats, which increases the chance of encountering pots and increases the probability of capture.

Survival was lower for larger octopus and females, possibly due to post-spawning senescence. The survival for this population was modeled using recaptures of mostly mature individuals (82% were at or above the size at maturity; Chapter 5). *E. dofleini* is known to be semelparous, with both females and males dying within weeks to months after reaching respective size at maturity (Chapter 5). As octopus senesce and die, they are no longer susceptible to capture which directly affects survival estimates. Female survival estimates may be lower than male survival due to sex-specific post-spawning reproductive activities. Just prior to spawning, female octopus will decrease their food intake (Wodinsky 1978) or stop feeding altogether (Gillespie et al. 1998), which would make it unlikely that they would be captured in baited pots, thereby decreasing survival estimates. As male *E. dofleini* have the potential to mate with more than one female (Anderson et al. 2002) and do not have to den-up to protect eggs, they probably need to move around more to find additional mates, which would increase their susceptibility to capture and increase survival (Hartwick 1983).

Decreasing survival rates of larger *E. dofleini* may also result from other behavioral changes. Large and mature octopus need to actively search for mates (Chapter 3), which may increase exposure to predation and decrease survival (Mather and O'Dor 1991). In the EBS there are a large number of predators on *E. dofleini* including: skate species (Orlov 1998), sleeper sharks (Yang and Page 1998), sea otters (Watt et al. 2000), harbor seals (Conners and Jorgensen 2008), and Steller sea lions (Merrick et al. 1997). Other possible causes for decreased survival with size are increased potential for incidental capture in fisheries (Chapter 3), competition for resources with conspecifics (Mather and O'Dor 1991), and increased susceptibility to disease (Anderson et al. 2002).

Estimates of mortality for *E. dofleini* are much higher than has been reported by federal

fisheries managers likely due to maturity status of larger octopus. My estimate for instantaneous mortality ($M = 3.40$) was very high due to the semelparity of large and mature octopus captured. Lower mortality estimates using Rikhter and Efanov's (1976) equation ($M = 0.53$; Conners et al. 2014) require an estimated age at maturity and account for octopus mortality throughout their lifespan. Though this estimate represents the best available data, there is currently no method to age *E. dofleini*, and therefore no way to ascertain that the age at maturity for *E. dofleini* is three years. As described above, *E. dofleini* are semelparous and die within months of mating, therefore, mortality will increase significantly once octopus reach maturity. As most of the *E. dofleini* captured in this study were likely mature and from the same region of the EBS where most of the commercial incidental catch occurs, a mortality estimate of 0.53 for this portion of the population is likely very low.

The abundance and density of *E. dofleini* in the study area were much higher than estimates reported in other areas of the range of this species. Beach-walk, SCUBA and submersible studies performed in Prince William Sound found octopus densities ranging from 0–2.5 octopus km^{-2} (Scheel 2002). In British Columbia values were higher than in Prince William Sound; SCUBA studies found octopus densities of 4.9 individuals km^{-2} and deeper water trap studies found densities of to 13.3 individuals km^{-2} (Hartwick et al. 1984). The larger density (127 octopus km^{-2}) of octopus in this study compared to others, is likely a function of high retention rates of *E. dofleini* in the study area (Chapter 3), which suggests that high quality habitat and abundant food may be available, making the study area suitable for relatively large numbers of individuals. Another possible explanation for lower densities reported in other areas may be related to the type of surveys being used. For both Scheel (2002) and Hartwick et al. (1984), visual surveys were used to locate this cryptic species in near-shore areas on beach-

walks, SCUBA, and submersible surveys, whereas collecting octopus in this study is likely more efficient.

My results suggest that the current biomass estimates for *E. dofleini* in the Bering Sea are overly conservative. Based upon Alaska Fisheries Science Center (AFSC) Bering Sea bottom trawl surveys, the 2014 biomass estimate for *E. dofleini* the entire Bering Sea shelf covering 1,300,000 km^2 (Marlow et al. 1994) was 2,095 mt (Conners et al. 2014). In this study, I estimated that the biomass of just three management areas in the Bering Sea covering 3,500 km^2 or 0.02% of the Bering Sea shelf was 20,697 mt. Traditional area-swept trawl methods to determine groundfish biomass are not appropriate for octopus because 1) trawls are inadequate for sampling rocky areas where octopus den, 2) octopus have the ability to escape trawl capture, and 3) trawls do not sample inshore areas where many octopus live (Conners et al. 2014). As part of the 2014 stock assessment for octopus, AFSC biologists estimated that annual predation on octopus by Pacific cod to be 3,452 mt (Conners et al. 2014). The Pacific cod predation estimate was used as a biological reference point to determine natural mortality and was set as the overfishing limit for octopus in the Bering Sea Aleutian Islands (Conners et al. 2014). However, Pacific cod represent only one of many predators on octopus and the size of beaks analyzed by federal fisheries managers suggest that the largest octopus were 1–2 kg (Conners et al. 2014). Both the bottom trawl surveys and the cod-stomach analysis methods appear to severely underestimate the population of octopus most susceptible to incidental capture, leading to an overly conservative estimate of octopus biomass in the EBS. Additionally, as groundfish pots may select for larger individuals and smaller octopus may be avoiding larger conspecifics (Conners et al. 2014), it is likely that total biomass is underestimated in this study considering smaller octopus weren't captured. Further studies using smaller pots or traps may be necessary

to estimate the biomass of smaller, immature *E. dofleini*.

Though the present study does not purport to estimate biomass or mortality for octopus for the entire Bering Sea shelf, the estimates presented here for a small area have implications for surrounding areas and serve as starting point for future studies. Further studies accounting for survival at different life-stages and linking octopus densities to habitat are required to expand the temporal and spatial scales of the estimates found in this study to better understand and appropriately manage this data poor species.

ACKNOWLEDGEMENTS

This study was supported by the North Pacific Research Board projects 906 and 1005, Alaska Sea Grant and National Oceanic and Atmospheric Administration. I would like to thank A. Seitz, E. Chenoweth, S. Tamone and A. Blanchard for reviewing this manuscript. I am also grateful to Z. Nehus, C. Stockton, K. Whittern, and T. Gibson for assistance in the field. Logistics and recapture support provided by the crew of the F/V St. Dominick.

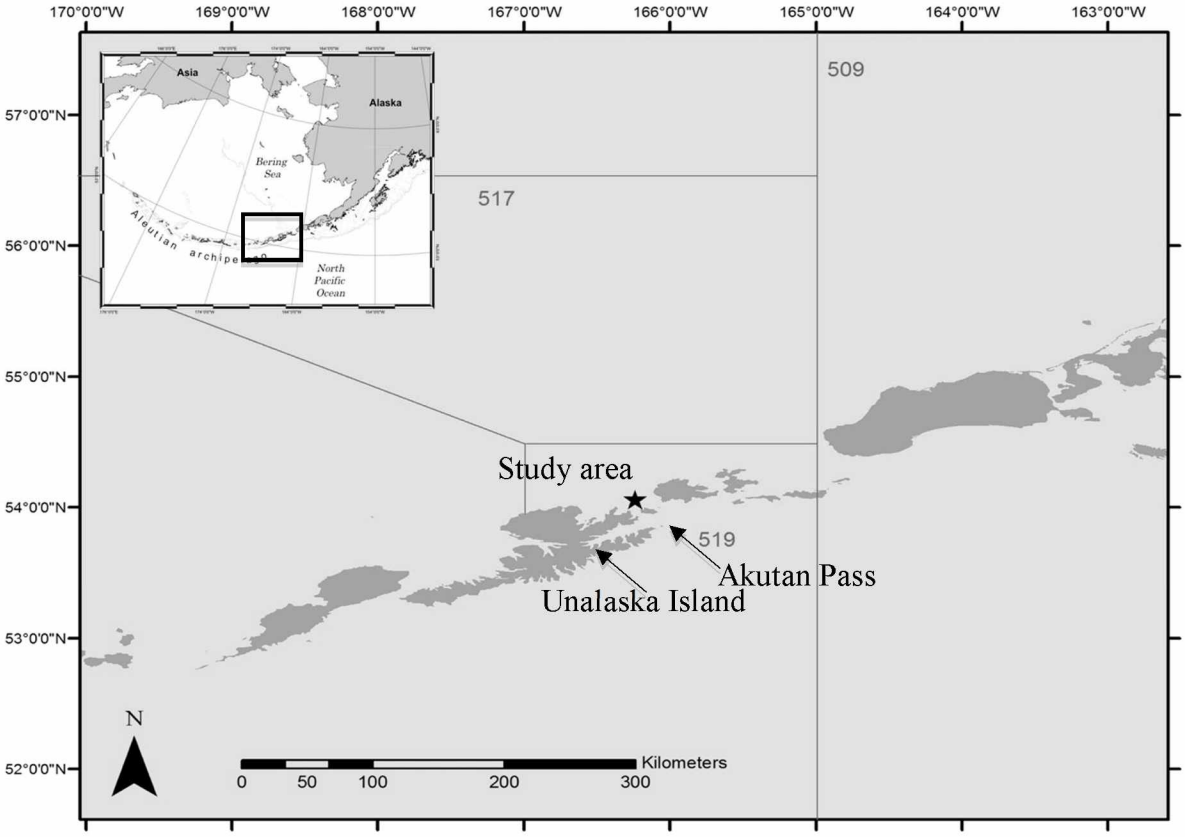


Figure 4.1. The 25 km^2 study area where *Enteroctopus dofleini* capture probability, survival and abundance estimates were examined. The study area measured 5 by 5 km and was located 20 km northeast of Unalaska Island, Alaska in the eastern Bering Sea. The star denotes the location of the study area and the boundaries of federal management areas 509, 517 and 519 are outlined

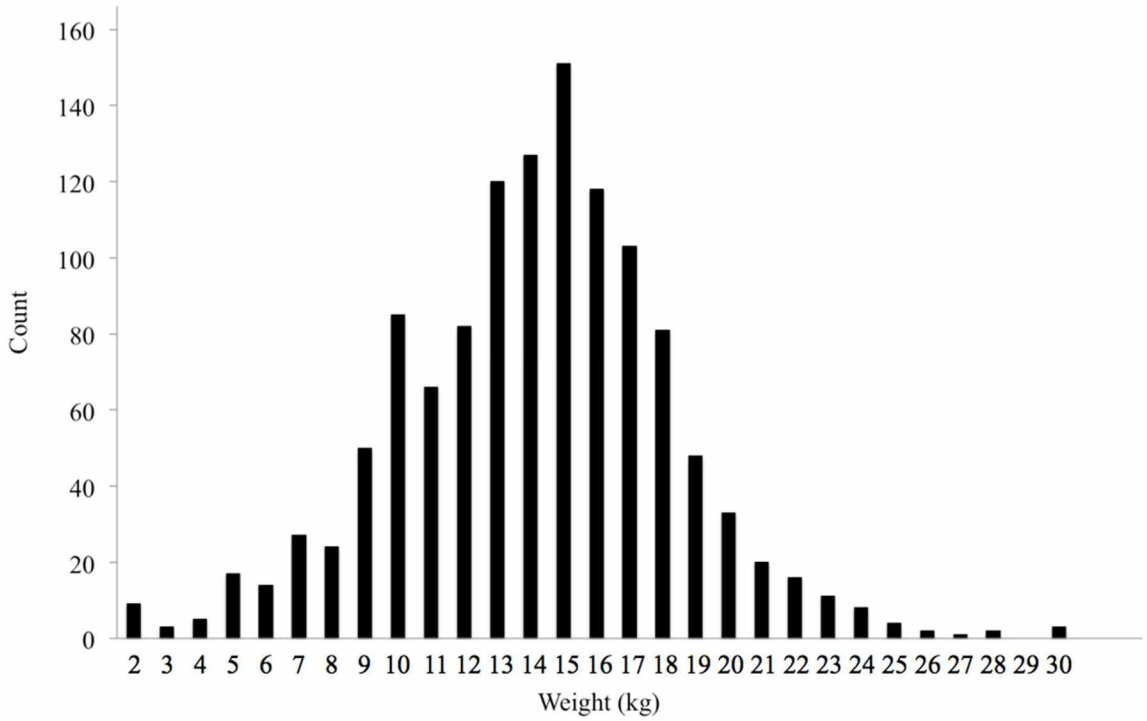


Figure 4.2. Size frequency of *Enteroctopus dofleini* captured and tagged in the eastern Bering Sea from 2009 to 2011 (n = 1,714)

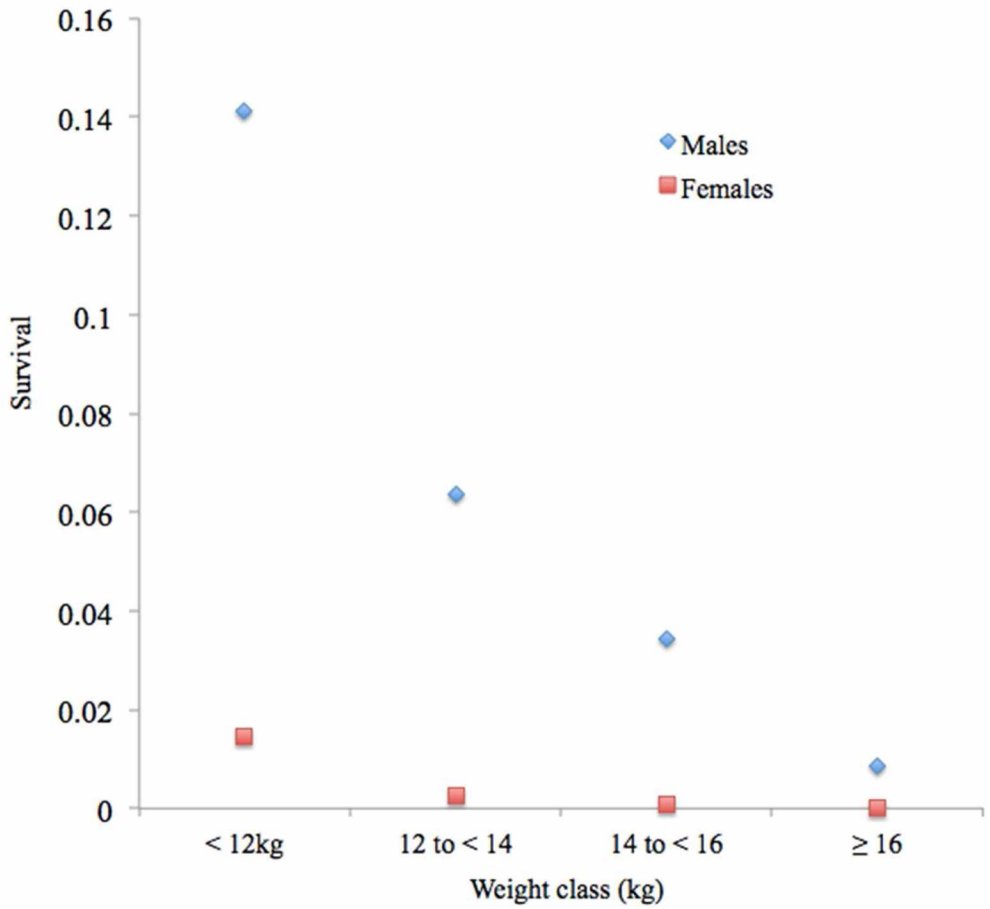


Figure 4.3. Decreasing annual survival with increasing weight for *Enteroctopus dofleini* in the eastern Bering Sea

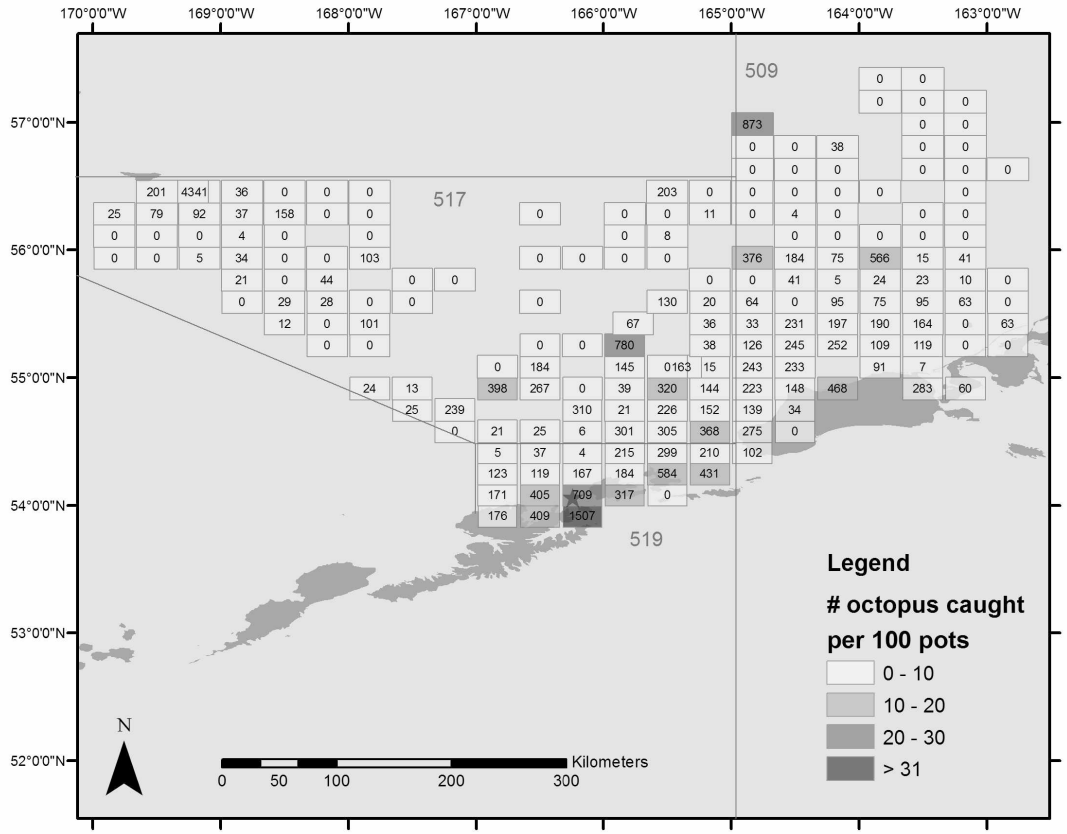


Figure 4.4. Federal fisheries observer 400 km^2 reference blocks showing the estimated biomass of *Enteroctopus dofleini* in the eastern Bering Sea. Shading of the boxes represents the mean octopus catch per 100 pots over the last 20 years with darker boxes representing greater number of individuals captured per 100 pots. The 400 km^2 federal observer block containing the study area has a star

Table 4.1. Summary of *Enteroctopus dofleini* release and recapture events from 2009 – 2011 in the eastern Bering Sea

		total releases	recapture periods					never recaptured
			10/27/09-11/17/09	1/1/10-3/24/10	9/7/10-10/21/10	1/2/11-6/1/11	9/10/11-10/21/11	
tagging periods	1. Autumn 10/27/09-11/17/09	244	17	8	5	0	0	214
	2. Spring 3/1/10-3/24/10	159		11	4	3	0	141
	3. Autumn 9/7/10-9/22/10	452			48	3	1	400
	4. Spring 1/2/11-3/7/11	286				37	1	248
	5. Autumn 9/10/11-10/20/11	573					108	465

Table 4.2. Top four combinations of probability of capture and survival models determined by Akaike Information Criterion (AIC). The top five capture covariates were modeled with constant survival, and the top five survival covariates were modeled with constant capture. All possible combinations of the 25 (5 capture x 5 survival) models were fitted to determine the final four models

Capture model	Survival model	AIC
(Intercept) +days +pots +weight	(Intercept) +sex +weight	228.78
(Intercept) +sex +weight	(Intercept) +weight	229.26
(Intercept) +sex +weight	(Intercept)	230.17
(Intercept)	(Intercept) +sex +weight	230.48

Table 4.3. Parameter estimates of the most parsimonious models for survival and probability of capture for *Enteroctopus dofleini* in the eastern Bering Sea

Survival	Estimate	SE
Intercept	1.874	0.646
Sex	0.916	0.368
Weight (kg)	-0.108	0.048
Capture	Estimate	SE
Intercept	-2.448	0.860
Days	0.078	0.033
Pots	0.535	0.224
Weight (kg)	-0.038	0.082

Table 4.4. Weight and sex-specific capture probability for *Enteroctopus dofleini* in the eastern Bering Sea. All weights are given in kilograms and A is autumn and S is spring

Weight class								
	Females				Males			
	<12	12 to <14	14 to <16	≥16	<12	12 to <14	14 to <16	≥16
A09 – S10	0.0676	0.0584	0.0545	0.0475	0.0667	0.0584	0.0541	0.0475
S10 – A10	0.1841	0.1618	0.1522	0.1370	0.1820	0.1619	0.1511	0.1345
A10 – S11	0.0918	0.0796	0.0744	0.0663	0.0906	0.0796	0.0738	0.0650
S11 – A11	0.0387	0.0333	0.0310	0.0257	0.0382	0.0333	0.0307	0.0270

Table 4.5. Sex and maturity-specific monthly and annual survival probability for *Enteroctopus dofleini* in the eastern Bering Sea. Immature females were less than 12.8 kg and immature males were less than 10.8 kg

Sex	Maturity status	Monthly survival ± SE	Annual survival ± SE
Female	Immature	0.6952 ± 0.0864	0.0128 ± 0.0057
Female	Mature	0.5530 ± 0.1137	0.0008 ± 0.0007
Male	Immature	0.8668 ± 0.0511	0.1799 ± 0.0371
Male	Mature	0.7462 ± 0.0917	0.0289 ± 0.0132

Table 4.6. Abundance estimates for *Enteroctopus dofleini* in the 25 km^2 study area 20 km northeast of Unalaska, Alaska between autumn 2009 and spring 2011

Time	Estimate	Standard Error
autumn 2009 – spring 2010	2789	1659
spring 2010 – autumn 2010	2997	2402
autumn 2010 – spring 2011	2995	2996

LITERATURE CITED

Amstrup SC, McDonald TL, Manly FJ. 2005. Handbook of Capture-Recapture Analysis. Princeton University Press, New Jersey

Anderson R, Wood J, Byrne R. 2002. Octopus senescence: the beginning of the end. J Appl Anim Welf Sci 5/4:275-283

Barry PD, Tamone SL, Tallmon DA. 2011. A comparison of tagging methodology for North Pacific giant octopus *Enteroctopus dofleini*. Fish Res 109:370–372

Boyle PR, Rodhouse P. 2005. Cephalopods: Ecology and Fisheries. Blackwell Publishers

Bush KL. 2006. ADF&G Regional Information Report. Project operation plan for Octopus Gear Study. Regional Information Report No 4K06, p. 35

Conners ME, Conrath C, Aydin K. 2012. Assessment of the Octopus Stock Complex in the Bering Sea and Aleutian Islands. North Pac. Fish. Mgmt. Council, Anchorage, AK

Conners ME, Conrath C, Aydin K. 2014. Assessment of the Octopus Stock Complex in the Bering Sea and Aleutian Islands. North Pac. Fish. Mgmt. Council, Anchorage, AK

Conners ME, Jorgensen E. 2008. BSAI Octopus Complex. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pac. Fish. Mgmt. Council, Anchorage, AK

Cooch E, White GC. 2005. Using MARK – a gentle introduction. Available from http://www.phidot.org/software/mark/docs/book/ [accessed 10 June 2012]

Fisheries and Oceans Canada. 2005. Pacific Region Octopus by Dive Experimental Harvest Guidelines. August 1, 2005 to July 31, 2006. 21pp

Gabe SH. 1975. Reproduction in the giant octopus of the North Pacific *Octopus dofleini martini*. Veliger 18:146-150

Gillespie GE, Parker G, Morrison J. 1998. A Review of Octopus Fisheries Biology and British Columbia Octopus Fisheries. Fisheries and Oceans Canada, issn 1480-4883

Hartwick EB. 1983. *Octopus dofleini*. In: Boyle PR (ed) Cephalopod Life Cycles. Vol 1. Species Accounts. Academic Press, London, pp 277-291

Hartwick EB, Ambrose RF, Robinson SMC. 1984. Dynamics of shallow-water populations of *Octopus dofleini*. Mar Biol 82:65-72. doi: 10.1007/BF00392764

Johnson TL. 2003. The Bering Sea and Aleutian Islands – Region of Wonders. Alaska Sea Grant, University of Alaska Fairbanks

Lebreton JD, Burnham KP, Clobert J, Anderson DR. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecol Monogr 62:67-118

Manly BFJ. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology 2nd edition. Chapman and Hall. London, UK

Marlow M, Cooper AK, Fisher MA. 1994. Geology of the eastern Bering Sea continental shelf. In: Geology of North America, pp 271-284

Mather JA, O'Dor RK. 1991. Foraging strategies and predation risk shape the natural history of Juvenile *Octopus vulgaris*. Bull Mar Sci 49(1-2):256-269

McDonald TL, Amstrup SC. 2001. Estimation of population size using open capture-recapture models. J Agric Biol Environ Stat 6(2):206-220

Merrick RL, Chumbley MK, Byrd GV. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. Can J Fish Aquat Sci 54(6):1342-1348

NMFS 2012. Bering Sea Aleutian Islands Catch Report through 31 December 2011, National Marine Fisheries Service

Orlov AM. 1998. The diets and feeding habits of some deep-water benthic skates (*Rajidae*) in the Pacific waters off the northern Kuril Islands and Southeastern Kamchatka. Alaska Fish Res Bull 5(1):1-17

Paust B. 1988. Fishing of Octopus: A guide for commercial fishermen. Alaska Sea Grant, Alaska

Pollock KH. 1982. A capture-recapture design robust to unequal probability of capture. J Wild Man 46:757-760

R Development Core Team, 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Rikhter VA, Efanov VN. 1976. On one of the approaches to estimation of natural mortality of fish populations. ICNAF Res. Doc., 79/VI/8

Scheel D. 2002. Characteristics of habitats used by *Enteroctopus dofleini* in Prince William Sound and Cook Inlet, Alaska. Mar Ecol 23(3):185-206

Scheel D, Bisson L. 2012. Movement patterns of giant Pacific octopuses, *Enteroctopus dofleini* (Wülker, 1910). J Exp Mar Biol Ecol 416-417:21-31. doi: 10.1016/j.jembe.2012.02.004

Watt J, Siniff DB, Estes JA. 2000. Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. Oecologia 124(2):289-298

White GC, Anderson DR, Burnham KP, Otis DL. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory Rep. LA-8787-NERP, Los Alamos, New Mexico, USA. 235pp

Wodinsky J. 1978. Feeding behavior of broody female *Octopus vulgaris*. Anim Behav 26:803-813

Yang MS, Page BN. 1999. Diet of Pacific sleeper shark, *Somniosus pacificus*, in the Gulf of Alaska. Fish Bull 97:406-409

CHAPTER FIVE

Seasonal sex-specific reproductive characteristics of the North Pacific giant octopus (*Enteroctopus dofleini*) in the Bering Sea[1]

ABSTRACT: Seasonal sex-specific maturity and body condition of the North Pacific giant octopus (*Enteroctopus dofleini*) were investigated to better understand the life history of this species at the northern extent of its range. From September 2010 to February 2012, I examined 195 *E. dofleini* captured 20 km northeast of Unalaska Island, Alaska (54° 04'N, 166° 25'W) to determine the reproductive ecology of this poorly understood species. Maturation, body condition, and reproductive activities were coupled to body size and seasonality. In autumn when temperatures were warmest, female *E. dofleini* had larger gonad and digestive gland weights relative to their total weight than similarly-sized females captured in the colder temperatures of winter and spring. Male *E. dofleini* showed no differences in any of these reproductive attributes among seasons. In the relatively cold temperatures of the Bering Sea, female and male *E. dofleini* attained 50% maturity at 12.8 kg and 10.8 kg respectively, while reports of *E. dofleini* in warmer and more southerly areas suggest maturity occurs at larger sizes indicating direct effects from water temperature on growth. Maturation of females must have occurred in autumn as mature females were not caught in later winter and spring, which suggests a winter spawning event. Maturation was most likely triggered by a combination of body size and environmental cues. The seasonal and sex-specific attributes reported here provide valuable life-history information that may result in changes to octopus populations with warming waters.

[1]Brewer RS, Norcross BL, Seitz AC, Blanchard AL. Submitted. Seasonal sex-specific reproductive characteristics of the North Pacific giant octopus (*Enteroctopus dofleini*) in the Bering Sea. J Moll Stud

INTRODUCTION

Enteroctopus dofleini in the Bering Sea is caught incidentally in Alaskan commercial groundfish fisheries in substantial numbers (Conners et al. 2014). Octopuses are semelparous, short-lived, and influenced by diet and temperature which makes defining life history parameters challenging (Ortiz et al. 2011). Size-at-maturity and seasonal patterns in maturity have been determined for many octopuses including *Eledone massyae* (Perez and Haimovici 1991), *Octopus bimaculoides* (Forsythe and Hanlon 1988), *O. mimus* (Cortez et al. 1995), *O. pallidus* (Leporati et al. 2008) and *O. vulgaris* (Otero et al. 2007). Sex-specific patterns in maturity have been determined for *E. moschata* (Sifner and Vrgoc 2009), *O. vulgaris* (Otero et al. 2007), *O. bimaculoides* (Forsythe and Hanlon 1988), and *O. pallidus* (Leporati et al. 2008). Variability in size-at-maturity and seasonality in maturity for both sexes may be a function of growth plasticity (Forsythe and Van Heukelem 1987), population abundances (Leporati et al. 2008), and/or lifespan (Boyle and Rodhouse 2005).

E. dofleini is a cold-water adapted species with a complicated reproduction cycle. It is found from California to Alaska to Japan at depths ranging from the intertidal to 344 m (Bernard 1970) and is the largest octopus species in the world (Hartwick et al. 1981). Mature male *E. dofleini* inseminate females with spermatophores using a specialized hectocotylized arm. Females can be inseminated before they are fully mature and can carry spermatophores inside their oviducts for days to months before their eggs are fertilized (Mottet 1975; Gabe 1975; Grubert and Wadley 2000). After fertilization, females search for suitable habitats and lay strings of eggs on the ceilings of rocky dens (Boyle and Rodhouse 2005). Just prior to spawning, female octopus decrease their food intake (Wodinsky 1978) or stop feeding altogether (Gillespie et al. 1998). The phenology of insemination, fertilization and spawning of *E. dofleini* in the wild

is not well known. In British Columbia, distinct seasonal reproductive cycles do not exist (Robinson 1983), with insemination likely occurring in autumn (Hartwick et al. 1978), and spawning occurring throughout the year (Hartwick 1983). In Japan, peak insemination occurs in November and December and peak spawning occurs from May to July, with spawning continuing through October (Kanamaru and Yamashita 1967). In the Gulf of Alaska, peak spawning occurs in winter months with other potential spawning events throughout the year (Conrath and Conners 2014). Though the post-spawning fate of wild male and female *E. dofleini* is unknown, laboratory studies suggest that males die shortly after insemination and females die after eggs hatch (Gabe 1975). The hatch time for *E. dofleini* is 150 days to almost a year after spawning, depending upon the water temperature (Kubodera 1991). *E. dofleini* spend up to 90 days as paralarvae before settling as benthic juveniles (Yamashita 1974). For most octopuses, including *E. dofleini*, age at maturity is unknown as octopuses have relatively few hard parts usable for aging and long-term tagging studies are limited (Chapter 2).

Maturation constitutes a key period where the production of eggs requires an increased energy demand. Octopuses rely on an organ called the digestive gland for the production of digestive enzymes and other functions. Because of its high lipid content, the digestive gland is also considered a potential storage organ for energy (Mangold and Bidder 1989) and the amount and kinds of lipids in the digestive gland may vary with nutritional condition (Blanchier and Boucaud-Camou 1984). For many octopuses, the size and content of the digestive gland is considered to be a proxy for body condition (Otero et al. 2004; Lourenco et al. 2012; Quetglas et al. 2011). Though it is generally accepted that the dietary lipids in the digestive gland play an important role for energy storage throughout the lifespan of most cephalopods (O'Dor and Wells 1978), there have been conflicting ideas as to the role of the digestive gland during reproduction.

For *O. mimus* and *O. hubbsorum*, digestive glands provide endogenous energy for gonad development as individuals are maturing (Cortez et al. 1995; Pliego-Cárdenas et al. 2011), while in *O. defilippi* and *O. vulgaris* maturation energy needs are met from exogenous resources (Rosa et al. 2004; Otero et al. 2007). For species that use endogenous resources for maturing gonads, gonad weight should be inversely proportional to digestive gland weight, while in species that use exogenous resources, both gonad weight and digestive gland weight should increase with maturity (Quetglas et al. 2011).

Unfortunately, the lack of information on the ecology of *E. dofleini* in the Bering Sea has hindered the ability for fisheries managers to assess the vulnerability of octopuses as by-catch in other directed fisheries (Conners et al. 2014). To better understand the life history of *E. dofleini* in the Bering Sea, I examined sex-specific seasonality of *E. dofleini* maturity over a period of two years. The specific objectives were 1) to determine sex-specific size at maturity for *E. dofleini*, 2) to analyze seasonal patterns of size and sex-specific maturity, and 3) to determine if the digestive gland is impacted by maturation of *E. dofleini*. This information will provide a first glimpse into the reproductive biology of *E. dofleini* in the Bering Sea, which may have implications for the seasonal capture of this species.

METHODS

Octopus were collected in the eastern Aleutian Islands, 20 km northeast of Unalaska Island, Alaska (center of study area at 54° 04'N, 166° 25'W; Fig. 5.1). The location is at the extreme southern end of the eastern Bering Sea continental shelf, a highly productive and diverse area supporting at least 450 species of fishes, crustaceans and mollusks, 50 species of seabirds and 25 species of marine mammals (Johnson 2003). The study area was approximately 20 km

northwest of Akutan Pass, a narrow shallow channel that allows the transfer of water between the Gulf of Alaska and the Bering Sea. In Akutan Pass the bi-directional flow of water and the relatively shallow sill (80 m) allow strong tidal currents to mix the water column from top to bottom creating a productive marine area (Stabeno et al. 2005).

Sampling gear was standard 2.5 x 2.5 x 0.9 m groundfish pots deployed in water depths ranging from 75 to 225 m during intermittent commercial fishing trips targeting Pacific cod (*Gadus macrocephalus*) between September 2010 and February 2012. Groundfish pots were baited with Pacific herring (*Clupea pallasii*) and soak time varied between 12 and 72 hours. After retrieval of pots, captured *E. dofleini* were removed and maintained individually in mesh bags placed in 1 x 1 m fish totes with circulating seawater. Each individual was delivered live to a laboratory in Unalaska, AK and was sacrificed and examined within 12 hours of capture.

Water temperature during each season was measured using HOBO Tidbit data loggers (Onset Computer Corp., Pocasset, MA, USA). Ten Tidbits were attached to randomly selected groundfish pots and temperature was recorded every hour while the pots were soaking. Groundfish pots with data loggers were deployed in autumn from September to December and in winter through spring from January to June. All temperatures recorded for a given month were averaged to determine monthly mean bottom water temperature. In this study three seasons were examined: autumn (September–November), winter (January–March), and spring (May–June).

Total body weight (TW), gonad weight (GW), and digestive gland weight (DGW) were determined after individuals were sacrificed. The TW of each *E. dofleini* was measured to the nearest 0.1 kg using hanging spring scales after water was drained from the octopus mantle cavity. The GW was measured to the nearest 0.001 kg using an electronic scale. The GW for females included the ovary and complete oviducal glands. The GW for males included the

testes, Needham's sac and penis. In a subsample of individuals captured in autumn and winter months, the digestive gland was removed and measured with an electronic scale to the nearest 0.001 kg. Each octopus was sexed by visual inspection of reproductive organs and maturity was determined by macroscopic inspection of the gonads. Maturity in females was clearly indicated by large yellow or orange ovaries (Pickford 1964; Perez and Haimovici 1991). Maturity in males was indicated by the presence of complete spermatophores in the Needham's sac (Pickford 1964; Perez and Haimovici 1991). The probability of maturity and GSI were examined among three seasons: autumn, winter and spring, while DGI was examined only in autumn and winter.

A gonadosomatic index (GSI) and a digestive gland index (DGI) was calculated to assess the weight of gonads and digestive glands relative to TW. The equation for GSI was GSI = $\frac{\text{GW}}{\text{TW}-\text{GW}}$ * 100, as described by Zghidi et al. (2004). The body condition of whole animals was determined by using the equation DGI = $\frac{\text{DGW}}{\text{TW}-\text{DGW}}$ * 100, as described by Castro et al. (1992); Cortez et al. (1995) and Otero et al. (2004). Regression analysis was performed with maturity and GSI as response variables and year, sex, season and TW as candidate explanatory variables. Regression analysis was also performed with DGI as a response variable and maturity, year, sex, season and TW as explanatory variables. Model selection was based on the Akaike information criterion (AIC), with the preferred model having the minimum AIC. Model selection led to the exclusion of "year" as a covariate in each of these models. Maturity was a binomial response variable requiring a logistic regression model. The size at 50% maturity for each sex was modeled by finding the point at which fitted values equaled 50% (Tafur et al. 2001):

$$P = \frac{1}{1+\exp[-(\alpha+\beta \text{TW})]}$$

where P represents the probability of maturity based on total weight (TW). For this calculation, α and β are regression parameters described by Tafur et al. (2001) and Leporati et al. (2008).

Statistical analysis was conducted in R (R Development Core Team 2010), significance levels were set at $\alpha = 0.05$ and all means are reported with ± SE unless otherwise noted.

RESULTS

A total of 195 *Enteroctopus dofleini* was analyzed in the laboratory with a mean weight of 12.2 kg ± 0.3. Ninety-two female *E. dofleini* were examined: 25 from autumn, 40 from winter, and 27 from spring. One hundred and three males were examined: 33 from autumn, 47 from winter, and 23 from spring. Seasonal total weights varied from 1.25 to 22.9 kg for females and 3.5 to 24.1 kg for males (Table 5.1).

The range of bottom temperatures over the three-year study was 3.53°C to 6.41°C, with the warmest temperatures in autumn and the coldest temperatures in winter. In autumn, mean monthly temperatures increased from 5.11°C in September to 5.81°C in November (Fig. 5.2). In winter, mean monthly temperatures decreased from 4.74°C in January to 3.53°C in March and in spring, mean monthly temperatures increased from 4.02°C in May to 4.46°C in June.

Total weight, season and sex were significant predictors of maturity with a significant season and sex interaction. For both sexes, larger *E. dofleini* were more likely to be mature than smaller *E. dofleini* (Table 5.2). For females, the probability of a captured individual being mature was significantly different among seasons, while for males there was no difference among seasons (Table 5.2). Of the females captured, 91.33% ± 0.06 were mature in autumn, 2.42% ± 0.06 were mature in winter, and 44.49% ± 0.06 were mature in spring (Fig. 5.2). Of the males captured, 69.73% ± 0.08 were mature in autumn, 59.62% ± 0.07 were mature in winter and 69.66% ± 0.10 were mature in spring (Fig. 5.2). The size at 50% maturity for females was 12.8 kg with mature females as small as 9 kg and immature females as large as 14.5 kg (Fig.

5.3). The size at 50% maturity for males was 10.8 kg with mature males as small as 9.4 kg and immature males as large as 15.5 kg (Fig. 5.3).

Total weight, season and sex were also significant predictors of the gonadosomatic index (GSI) with a significant season and sex interaction. Larger *E. dofleini* tended to have a higher GSI than smaller *E. dofleini* (Table 5.3). The GSI of female *E. dofleini* was significantly different among seasons, while the GSI of male *E. dofleini* was not (Table 5.3). The mean GSI of females was 6.36 ± 0.42 in autumn, 1.46 ± 0.15 in winter and 2.82 ± 0.39 in spring (Fig. 5.4). The mean GSI of males was 6.42 ± 0.36 in autumn, 6.14 ± 0.38 in winter and 7.06 ± 0.60 in spring (Fig 5.4).

Maturity, season and sex were significant predictors of the digestive gland index (DGI) with a significant season and sex interaction and a significant maturity and sex interaction (Table 5.4). Total weight was not a predictor of the DGI despite being a predictor for maturity and GSI (Students t-test, $t = -0.791$, $p = 0.431$). The DGI of female *E. dofleini* was significantly different seasons, while the DGI of male *E. dofleini* was not (Table 5.4). The mean DGI of females was 6.04 ± 0.30 in the autumn and 4.31 ± 0.15 in the winter. The mean DGI of males was 3.38 ± 0.21 in the autumn and 3.71 ± 0.18 in the winter (Fig. 5.5). The DGI of female *E. dofleini* increased with maturity, while the DGI of male *E. dofleini* was not significantly related to maturity (Table 5.4). The mean DGI for females was 4.30 ± 0.16 for immature individuals and 5.85 ± 0.30 for mature individuals (Fig. 5.5). The mean DGI for males was 3.93 ± 0.29 for immature individuals and 3.45 ± 0.14 for mature individuals (Fig. 5.5).

DISCUSSION

Population fitness may be challenged by rapid environmental change, as is occurring in the Arctic where unprecedented warming has occurred. To maintain fitness, species and organisms must be adaptive to the changes experienced. One pathway for altered population dynamics is the relationship between maturation and seasonality. Potential sources of stress on a population include seasonal differences in maturity patterns caused by differences in food availability, and effects of warming temperatures on metabolic processes or the timing of egg hatching. Sex-specific maturity patterns may be the result of differences in pre-and/or post-reproductive activities. Though this study was not able to directly determine seasonal insemination and fertilization *in situ*, analyzing patterns in maturity of animals is a good proxy with which to infer reproductive status for octopus (Zghidi et al. 2004). I therefore use patterns in octopus maturity to infer reproductive status in *E. dofleini* in the Bering Sea.

Sex-specific reproductive ecology influences seasonality in *E. dofleini* maturation and reproduction. For female *E. dofleini*, maturity usually coincides with a decrease or cessation of feeding which radically slows or stops growth (Gillespie et al. 1998). As I captured octopus with baited pots, the collection of mature females in autumn suggests that they were still feeding, while the lack of mature females captured in winter and spring suggests that they were not feeding in those seasons. The deduction of winter spawning for *E. dofleini* in the Bering Sea is corroborated by back-calculation of breeding dates from published densities and development rates of paralarvae. *E. dofleini* paralarvae are most prominent in the Aleutian Islands from June to August suggesting a winter spawning season (Kubodera 1991). For male *E. dofleini* that have the potential to carry up to 15 spermatophores, the potential to mate with more than one female and not having to produce and protect eggs for months might account of the capture of mature

individuals in all seasons, and reduced apparent seasonality. For a cryptic and sometimes sparsely distributed population with a potentially low frequency of interaction, a longer period of maturation for males may positively impact contributions to post-reproduction success. Seasonality for *E. dofleini* maturity in Japan, British Columbia and the Gulf of Alaska, range from autumn to early spring (Kanamaru and Yamashita 1967; Hartwick et al. 1978; Conrath and Conners 2014). Seasonal maturity has also been documented for closely related confamilial species such as *Octopus vulgaris* (Zghidi et al. 2004; Otero et al. 2007) and *O. pallidus* (Leporati et al. 2008).

A larger size at maturity may reflect the greater investment in reproductive success for female octopus. The transition to maturity is an abrupt event when females reach a critical size (Otero et al. 2007) and as with other octopuses, female *E. dofleini* reached maturity at larger sizes than males. At least 50% of females that reached 12.8 kg by late autumn were mature and had the potential to spawn. This critical size may be important for egg production (Leporati et al. 2008), or the later protection of eggs (Steer et al. 2003). As with *E. dofleini*, larger size at maturity for females compared to males has also been observed in *Eledone moschata* (Sifner and Vrgoc 2009), *O. vulgaris* (Otero et al. 2007), *O. bimaculoides* (Forsythe and Hanlon 1988), and *O. pallidus* (Leporati et al. 2008).

A smaller size at maturity may reflect a difference in gonadal investment and post-spawning activities for male octopus. Once male octopus reach maturity, they will continue to produce spermatophores until they mate and ultimately die (Mangold 1983). As *E. dofleini* may live 2 to 5 years (Hartwick 1983), the continual addition of spermatophores over time might explain the presence of mature males in each season, a reproductive strategy enhancing overall success for a dispersed population with potentially low probabilities of interspecific interactions,

particularly in marginal habitats. As females can store sperm prior to maturity, early maturation for males may allow for opportunistic mating with similar sized immature females (Joll 1976), increasing population fitness by increasing the probability of insemination.

Warmer water temperatures can increase growth rates (Forsythe and Hanlon 1988) and conversion efficiencies of food (Rigby and Sakurai 2004) thus leading to differences in size at maturity. As expected, the size at 50% maturity for female and male *E. dofleini* in the Bering Sea was smaller than those from more southerly, warmer locations. In Japan, where the mean water temperature was approximately 10°C, *E. dofleini* are mature at 15–20 kg (Mottet 1975, Rigby and Sakurai 2004). In British Columbia where the mean temperature was approximately 8°C, females mature at sizes greater than 12.5 kg and male *E. dofleini* mature at 12.5 kg (Robinson 1983). In the Gulf of Alaska where mean temperatures are approximately 7°C, size at maturity for both female and male *E. dofleini* was 14 kg (Conrath and Conners 2014). In this Bering Sea-based study, the mean temperature was approximately 5°C, with females maturing at 12.8 kg and males at 10.8 kg. The northern limit of this species' distribution is not known, so there may be populations in colder waters that mature at smaller sizes. The inverse latitudinal gradient in size at maturity for *E. dofleini* appears to be a result of warmer water in southerly latitudes, although upper and lower thermal limits are unknown. Unfortunately, there are no documented techniques to age *E. dofleini* so determination of temperature effect on age at maturity is impractical. Nevertheless, observational data suggest that colder water temperatures directly influence individual growth dynamics, but do not negatively affect abundance in the eastern Bering Sea. Some benthic octopuses are present in the northeastern Chukchi Sea as well (A. Blanchard, personal communication) suggesting that temperature alone may not prevent this mollusk from inhabiting colder waters. Thus, *E. dofleini* reproductive ecology in the eastern

Bering Sea may adapt to water temperature variations expected with continued climate warming, although upper temperature limits may inhibit success of more southerly populations.

Energetic investment in digestive glands is a function of sex-specific reproductive ecology. Prior to producing gonads, immature female and male *E. dofleini* are likely bioenergetically similar as energy fuels somatic growth (Rosa et al. 2004). As octopus mature, there is a switch from somatic growth to gamete production and energy is re-allocated to reproductive activities (Rodhouse 1998). Since DGI did not decrease with maturity for either males or females, it is likely that the energy for gonad development did not come at the expense of the digestive gland. The production of gonads for *E. dofleini* is likely fueled by exogenous resources. Similarly, biochemical analyses of several temperate octopuses have shown that reproductive processes do not rely on energy from stored reserves, but rather on direct energy inputs from feeding (Rosa et al. 2004). However, for many species of octopus, the role of digestive gland in octopus maturation is poorly understood (Quetglas et al. 2011)

The increase in DGI for mature females and the lack of increase in DGI for mature males may reflect post spawning needs for females. The digestive gland may serve as the primary source of energy in the final months of a female's life after egg spawning, when she is brooding eggs and no longer feeding (Pollero and Iribarne 1988; Castro et al. 1992; Otero et al. 2007). Therefore, increased size and hence energy content of the digestive gland may directly benefit females by supporting brooding. Unfortunately, no senescent females were captured in this study; therefore, I was unable to test for the expected decrease in female digestive gland associated with starvation after fertilization. In contrast to females, males do not brood eggs, so the potential need for the digestive gland to sustain life over that period of time is inconsequential. It is possible that once an octopus begins to access nutrition from the digestive

gland, a sequence of events takes place that ultimately leads to the demise of the organism. For females, the larger digestive gland may sustain octopus though the brooding phase. As with *E. dofleini*, the larger investment in the digestive gland by females compared to males has been observed in *O. vulgaris* (Rosa et al. 2004; Otero et al. 2007) and *O. defilippi* (Rosa et al. 2004).

The roles of body size and environmental cues in triggering maturation in *E. dofleini* are not clearly known. My study suggests that a combination of size and timing may instigate maturity for *E. dofleini* in the Bering Sea, though covariances in growth, reproduction, and seasonality confound accurate inferences. The presence of mature *E. dofleini* in autumn may reflect an "optimal spawning period," such as noted in *O. pallidus* (Leporati et al. 2008) when biological and environmental factors like temperature may be most beneficial for reproductive investment after a successful summer feeding period. The timing of maturity, and thus spawning, may also influence success of *E. dofleini* offspring that hatch months later. In Japan, where temperatures are warmer, peak paralarval densities of *E. dofleini* were found in spring when primary production was high (Mottet 1975). In the Aleutian Islands, peak densities occur later in the year from June to August, a period that also coincides with high primary production and warmer water (Kubodera 1991). Temperature directly controls the onset of sexual maturity in some species of octopus (Van Heukelem 1976; Forsythe and Hanlon 1988; Ortiz et al. 2011) and may restrict breeding times of others (Grubert and Wadley 2000). For octopuses, once a minimum weight is reached, biological and environmental variables may collectively modulate reproductive and somatic investment (Lourenco et al. 2012). The strong seasonal signal in the reproductive ecology of *E. dofleini* in the eastern Bering Sea indicates a coupling with, and potentially a modulation of, biological processes by environmental cues.

Marine invertebrates, including *E. dofleini*, appear to be highly tolerant of temperature variations and adaptable to wide ranging environmental conditions. The bivalve *Mytilus trossulus*, for example, ranges from coastal waters of the North Pacific in California to the Chukchi Sea at Point Barrow, and its reproductive ecology is adapted to the variations in seasonality throughout this distribution (Blanchard and Feder 1997; Blanchard 2014). Other marine invertebrates adjusting to wide climatic conditions include the intertidal barnacle *Semibalanus balanoides* and numerous subtidal bivalves and polychaete worms. In light of the potentially wide environmental tolerances, management of marine species under rapidly changing environmental conditions in Alaska's sub-arctic seas is challenging. Interactions between physiological and ecological effects from warming waters increases the potential for exacerbated negative impacts on marine fauna and ecosystems through multiple stressors (e.g., Blanchard and Feder 2003). The reproductive ecology of *E. dofleini* suggests adaptability to warmer waters, with direct influences in individual growth and success. Of concern in the changing environment is the re-allocation of energy from reproduction to somatic growth and a potential mismatch in the timing of seasonal cycles and food availability. The role of *E. dofleini* in the ecosystem and potential responses to warming waters is thus suggested as a need for further research.

In summary, the present study shows that the seasonality of reproduction in *E. dofleini* has important consequences for their ecology. In the eastern Bering Sea, female *E. dofleini* mature in autumn, are inseminated and spawn in winter, and have eggs hatching in late spring to summer. This pattern may result from the availability of food resources in autumn and/or the hatch timing of *E. dofleini* paralarvae into the pelagic ecosystem when primary production is at its height. Males are reproductively active over a longer time period than females, possibly

reflecting differences in sex-specific gonadal investment or post-spawning activities. Maturation and reproductive activities of *E. dofleini* are likely triggered by a combination of both body size and environmental cues.

There is a potential to alter the ecological processes that may impact the lifecycles of marine organisms with increased climate warming. For *E. dofleini,* warming temperatures may not only increase size at maturity in the Bering Sea, as found in other regions, but it may also reduce the time for eggs to hatch. This may result in a mismatch between hatching paralarvae and summer primary production and a shift in timing for maturation of gonads in *E. dofleini*. Further studies are needed to determine the exact effects of increased water temperatures on the success of *E. dofleini* reproduction.

ACKNOWLEDGEMENTS

I would like to thank Ellen Chenoweth, Sherry Tamone, Sarah Brewer, and Melissa Good for reviewing this manuscript. I am also grateful to Zach Nehus, Chaz Stockton, Keith Whittern, and Troy Gibson for assistance in the field. Logistics and captures were provided by the crew of the F/V St. Dominick. This study was supported by the North Pacific Research Board Grant numbers 0906 and 1005.

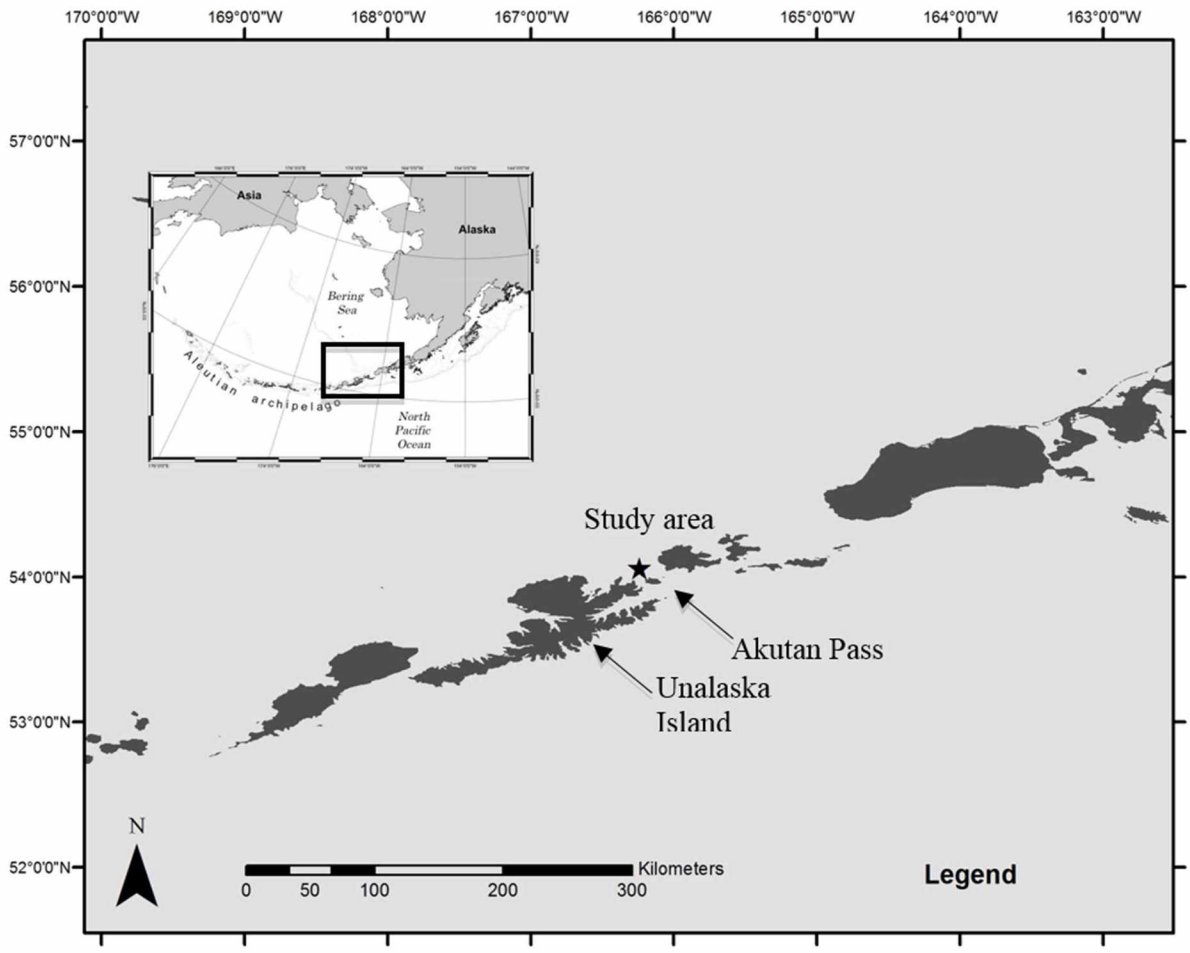


Figure 5.1. The study area measured 5 by 5 km and was located 20 km northeast of Unalaska Island, AK

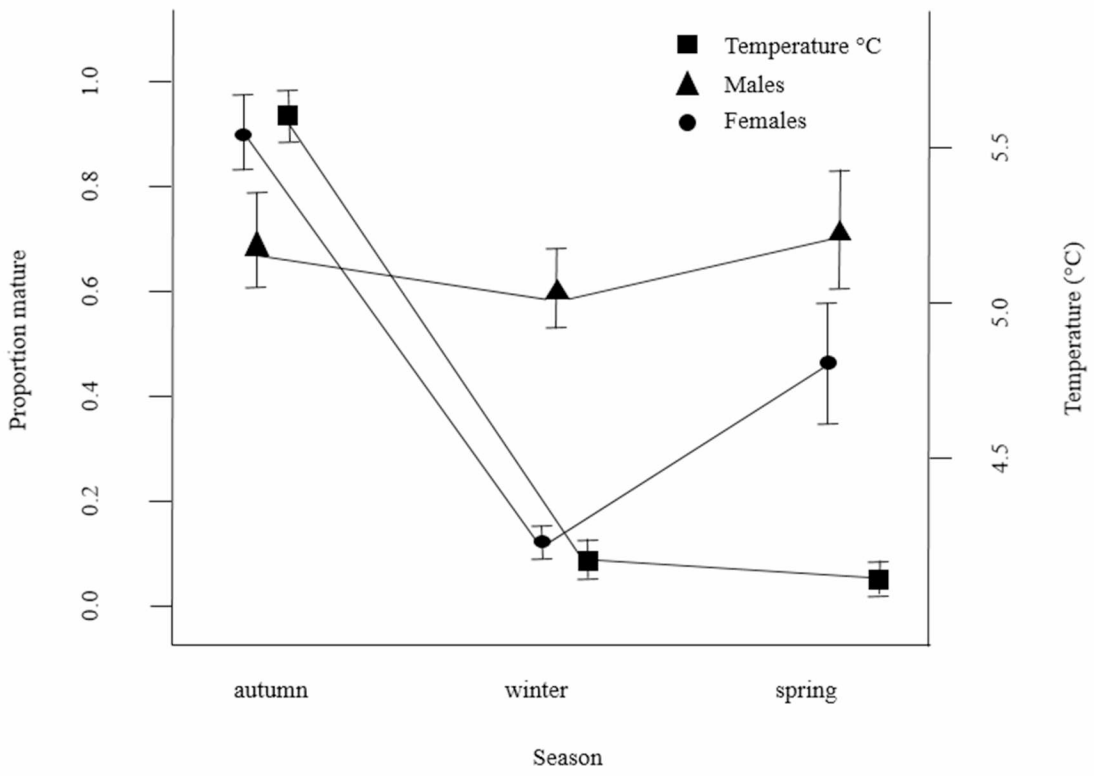


Figure 5.2. Proportion of mature *Enteroctopus dofleini* captured in the eastern Bering Sea varied with season and sex. Mean temperature (°C) is plotted in each season

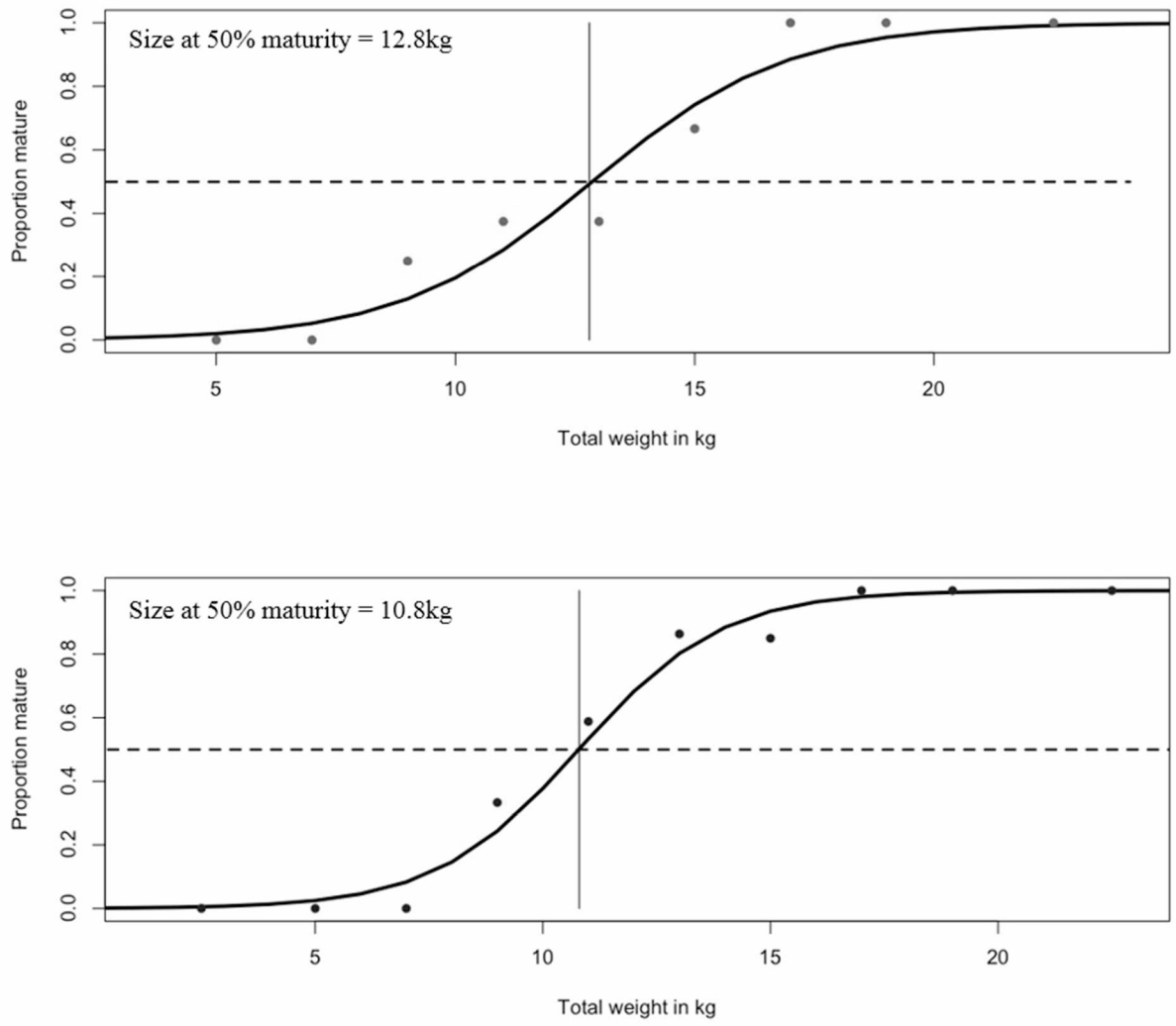


Figure 5.3. Proportion of mature *Enteroctopus dofleini* in relation to total weights for females (top) and males (bottom). The vertical line delineates the weight at which 50% of the individuals in the population were mature

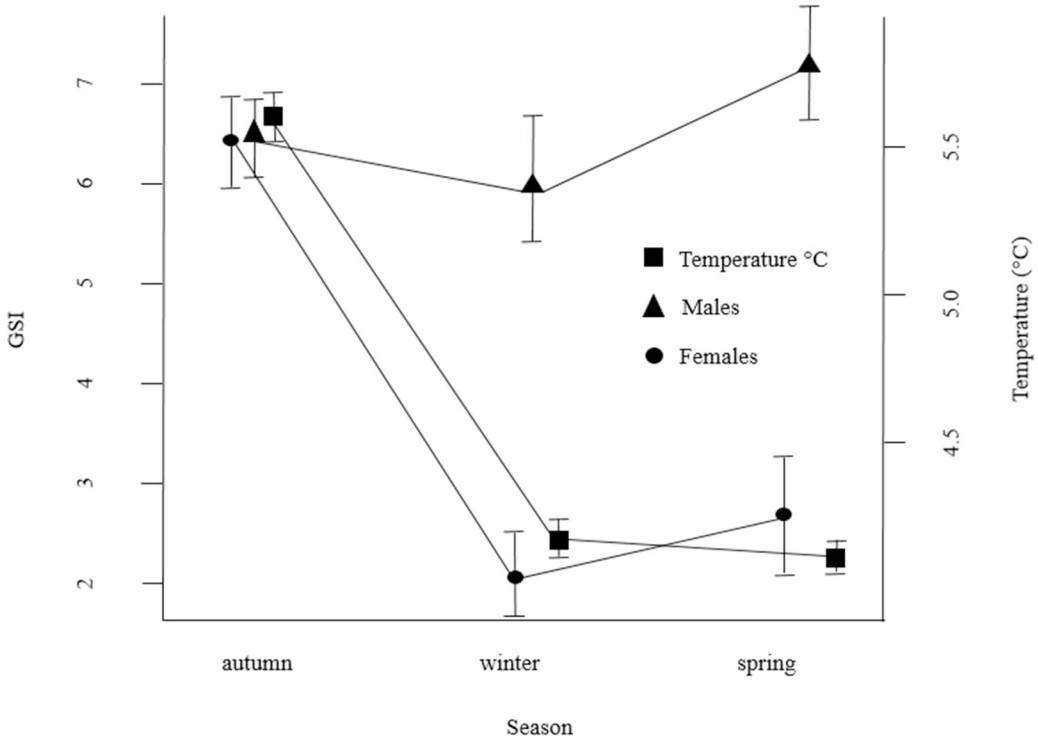


Figure 5.4. Gonadosomatic index (GSI) for *Enteroctopus dofleini* captured in the eastern Bering Sea varied with season and sex. Mean temperature (°C) is plotted in each season

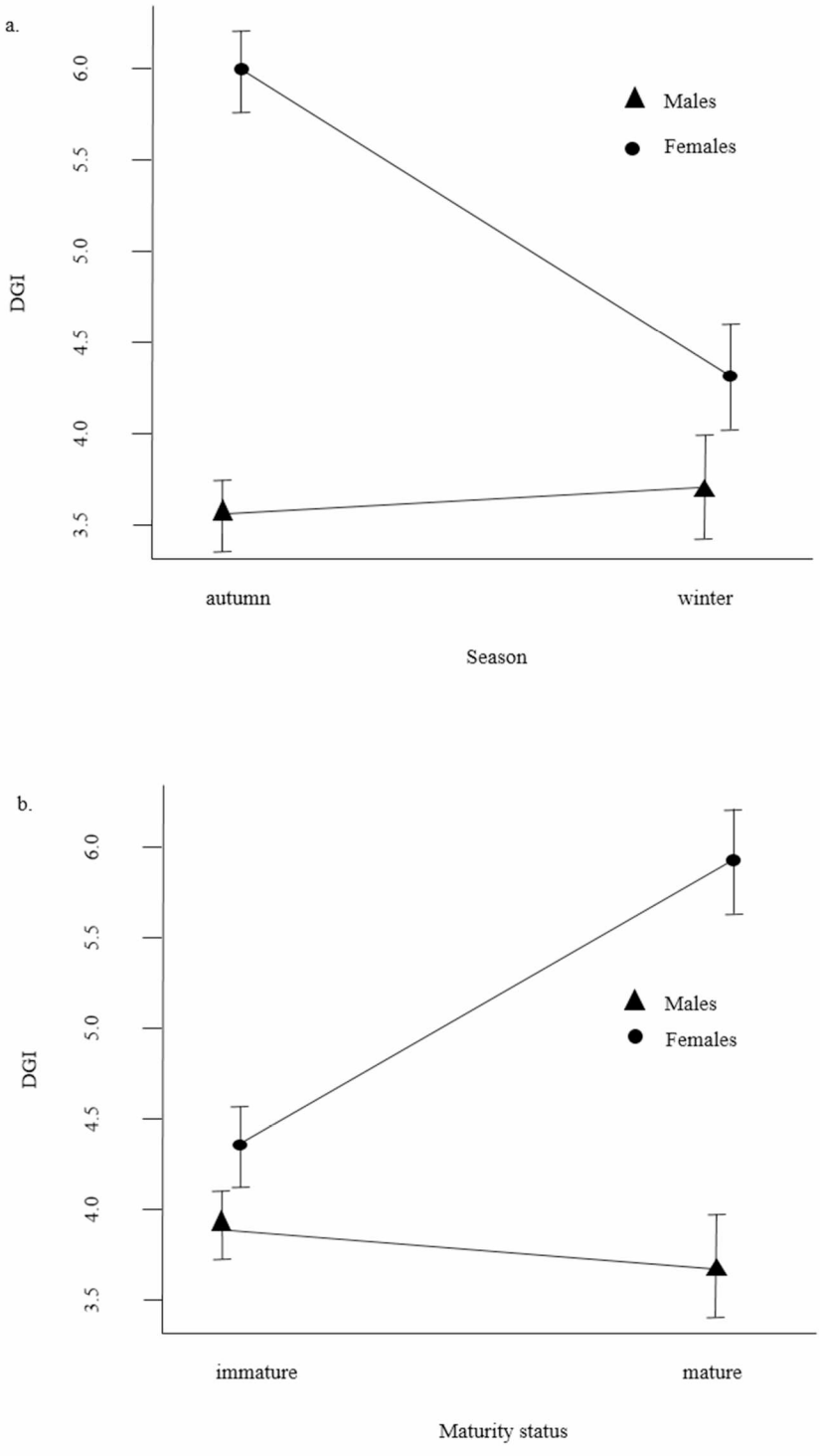


Figure 5.5. Relationship between digestive gland index (DGI) and (a) season and (b) maturity status for *Enteroctopus dofleini*

Table 5.1. Mean total weight, probability of maturity for male and female *Enteroctopus dofleini* captured in each of three seasons. Probability of maturity is based on capturing a 12.2 kg *E. dofleini*

	Females			Males		
	N	TW (kg ± SE)	Probability of maturity	N	TW (kg ± SE)	Probability of maturity
Autumn	25	12. 3± 0.6	0.95	33	13.2 ± 0.6	0.57
Winter	40	11.0 ± 0.4	0.02	47	12.0 ± 0.5	0.74
Spring	27	12.3 ± 1.0	0.50	23	12.6 ± 1.0	0.82

Table 5.2. Parameters, estimates (*B*), standard errors (*SE*), test results (*z-value*), and significance levels (*P*) of GLM analysis for the expected maturity of *Enteroctopus dofleini* in the Bering Sea

Parameter	*B*	*SE*	*z-value*	*p*
Intercept	-8.183	1.685	-4.856	<0.001
Total weight	0.694	0.123	5.654	<0.001
Winter	0.762	0.722	1.055	0.291
Spring	1.246	0.845	1.474	0.141
Females	2.690	1.034	2.601	0.009
Winter: Females	-7.768	1.663	-4.670	<0.001
Spring: Females	-4.220	1.360	-3.103	0.002

Table 5.3. Parameters, estimates (*B*), standard errors (*SE*), test results (*t-value*), and significance levels (*P*) of GLM analysis for the gonadosomatic Index (GSI) of *Enteroctopus dofleini* in the Bering Sea

Parameter	*B*	*SE*	*t-value*	*p*
Intercept	2.180	0.634	3.438	<0.001
Total weight	0.320	0.039	8.146	<0.001
Winter	0.148	0.475	0.313	0.755
Spring	0.846	0.565	1.497	0.136
Females	0.036	0.565	0.063	0.949
Winter: Females	-3.812	0.717	-5.316	<0.001
Spring: Females	-4.171	0.816	-5.110	<0.001

Table 5.4. Parameters, estimates (*B*), standard errors (*SE*), test results (*t-value*), and significance levels (*P*) of GLM analysis for the digestive gland index (DGI) of *Enteroctopus dofleini* in the Bering Sea

Parameter	*B*	*SE*	*t-value*	*p*
Intercept	6.226	0.646	9.645	<0.001
Season	-1.992	0.645	-3.086	0.003
Maturity	-0.206	0.644	-0.319	0.751
Sex	-1.865	0.613	-3.043	0.003
Season:Maturity	1.123	0.583	1.925	0.058
Season:Sex	1.457	0.583	2.497	0.015
Maturity:Sex	-1.100	0.557	-1.974	0.050

LITERATURE CITED

Bernard FR. 1970. A distributional checklist of the marine mollusks of British Columbia: based on faunistic surveys since 1950. Syesis 3:75-94

Blanchard AL. 2014. Variability of macrobenthic diversity and distributions in Alaskan sub-Arctic and Arctic marine systems: a review of long-term environmental studies in Alaska. Mar Biodivers 45:781-795

Blanchard A, Feder HM. 1997. Reproductive timing and nutritional storage cycles of *Mytilus trossulus* Gould, 1850, in Port Valdez, Alaska, site of a marine oil terminal. Veliger 40:121-130

Blanchard A, Feder HM. 2003. Adjustment of benthic fauna following sediment disposal at a site with multiple stressors in Port Valdez, Alaska. Mar Pollut Bull 46:1590-1599

Blanchier B, Boucaud-Camou E. 1984. Lipids in the digestive gland and the gonad of immature and mature Sepia officinalis (Mollusca: Cephalopoda). Mar Biol 80:39–43

Boyle PR, Rodhouse P. 2005. Cephalopods: Ecology and Fisheries. Blackwell Publishers

Castro BG, Garrido JL, Sotelo CG. 1992. Changes in composition of digestive gland and mantle muscle of the cuttlefish *Sepia officinalis* during starvation. Mar Biol 114:11-20

Conners ME, Conrath C, Aydin K. 2014. Assessment of the Octopus Stock Complex in the Bering Sea and Aleutian Islands. North Pac. Fish. Mgmt. Council, Anchorage, AK

Conrath CL, Conners ME. 2014. Aspects of the reproductive biology of the North Pacific giant octopus (*Enteroctopus dofleini*) in the Gulf of Alaska. Fish Bull 112:253-260

Cortez T, Castro BG, Guerra A. 1995. Reproduction and condition of female *Octopus mimus* (Mollusca: Cephalopoda). Mar Biol 123:505-510

Forsythe JW, Hanlon RT. 1988. Behavior, body patterning and reproductive biology of *Octopus bimaculoides* from California. Malacologia 29:41-55

Forsythe JW and Van Heukelem WF. 1987. In: Boyle PR (ed) Cephalopod Life Cycles. Vol. 2. Growth. Academic Press, London, pp 135-156

Gabe SH. 1975. Reproduction in the giant octopus of the North Pacific *Octopus dofleini martini*. Veliger 18:146-150

Gillespie GE, Parker G, Morrison J. 1998. A Review of Octopus Fisheries Biology and British Columbia Octopus Fisheries. Fisheries and Oceans Canada, issn 1480-4883

Grubert MA, Wadley VA. 2000. Sexual maturity and fecundity of *Octopus maorum* in Southeast Tasmania. Bull Mar Sci 66:131-142

Hartwick EB. 1983. *Octopus dofleini*. In: Boyle PR (ed) Cephalopod Life Cycles. Vol 1. Species Accounts. Academic Press, London, pp 277-291

Hartwick EB, Thorarinsson G, Tulloch L. 1978. Antipredator behaviour in *Octopus dofleini* (Wülker). Veliger 21:263-26

Hartwick EB, Tulloch L, Macdonald S. 1981. Feeding and growth of *Octopus dofleini* (Wülker). Veliger 24:129-138

Johnson TL. 2003. The Bering Sea and Aleutian Islands – Region of Wonders. Alaska Sea Grant, University of Alaska Fairbanks

Joll LM. 1976. Mating, egg-laying and hatching of *Octopus tetricus* in the laboratory. Mar Biol 36:327-333

Kanamaru S, Yamashita Y. 1967. Investigations of the Marine Resources of Hokkaido and Developments of the Fishing Industry 1961-1965. Report of the Hokkaido Marine Research Center, 32 pp

Kubodera T. 1991. Distribution and abundance of the early life stages of octopus, *Octopus dofleini* in the North Pacific. Bull Mar Sci 49:235-243

Leporati SC, Semmens JM and Pecl GT. 2008. Reproductive status of *Octopus pallidus* and its relationship to age and size. Mar Biol 155:375-385

Lourenco S, Moreno A, Narciso L, Gonzalez AF, Pereia J. 2012. Seasonal trends of the reproductive cycle of *Octopus vulgaris* in two environmentally distinct coastal areas. Fish Res 127-128:116-124

Mangold K, Bidder AM. 1989. L'appareil digestif et la digestion. In: Traité de zoologie. Anatomie systématique, biologie: céphalopodes. Tomo V. Fascicule 4. Masson, Paris, 321–373

Mangold K. 1983. *Octopus vulgaris*. In: Boyle PR (ed) Cephalopod Lifecycles, Vol I, Academic Press, London, pp 335-364

Mottet, MG. 1975. The fishery biology of *Enteroctopus dofleini*. State of Washington Department of Fisheries management and research division. Technical Report 16

O'Dor RK, Wells MJ. 1978. Reproduction versus somatic growth: Hormonal control in *Octopus vulgaris*. J Exp Biol 77:15–31

Ortiz N, Re ME, Marquez F, Glembocki NG. 2011. The reproductive cycle of the red octopus *Enteroctopus megalocyathus* in fishing areas Northern Patagonian coast. Fish Res 110:217-223

Otero J, González AF, Regueira M, Garci ME. 2004. Reproductive biology of *Octopus vulgaris* in an upwelling area (NE Atlantic). ICES CM 2004/CC:01

Otero J, González AF, Sieiro MP, Guerra A. 2007. Reproductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. Fish Res 85:122-129

Perez JAA, Haimovici M. 1991. Sexual maturation and reproductive cycle of *Eledone massyae*, in Southern Brazil. Bull Mar Sci 49:270-279

Pickford GE. 1964. *Octopus dofleini*. Bull Bingham Oceanogr Coll 19:1-70

Pliego-Cárdenas R, García-Dominguez FA, Ceballos-Vázquez BP, Villalejo-Fuerte M, Arellano-Martinex M. 2011. Reproductive aspect of *Octopus hubbsorum* (Cephalopoda:

Octopodidae) from Espíritu Santo Island, southern Gulf of California, Mexico. Cienc Mar 37:23-32

Pollero RJ, Iribarne OO. 1988. Biochemical changes during the reproductive cycle of the small Patagonian octopus, *Octopus tehuelchus*, D'Orb. Comp Biochem Physiol 90:317-320

Quetglas A, Ordines F, Valls F. 2011. What drives the seasonal fluctuations of body condition in a semelparous income breeder octopus? Acta Oecol 37(5):476-483

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.Rproject.org, accessed 10 February 2013

Rigby PR, Sakurai Y. 2004. Temperature and feeding related growth efficiency of immature octopuses *Enteroctopus dofleini*. Suisanzoshoku 52(1):29-36

Robinson SMC. 1983. Growth of the giant Pacific octopus (*Octopus dofleini martini*) on the west coast of British Columbia. MS thesis, Simon Fraser University, Canada

Rodhouse PG. 1998. Physiological progenesis in cephalopod molluscs. Biol Bull 195:17–20

Rosa R, Costa PR, Nunes ML. 2004. Effect of sexual maturation on the tissue biochemical composition of *Octopus vulgaris* and *Octopus defilippi*. Mar Biol 145:563-574

Sifner SK, Vrgoc N. 2009. Reproductive cycle and sexual maturation of the musky octopus *Eledone moschata* in the northern and central Adriatic Sea. Sci Mar 73:439-447

Stabeno PJ, Kachel DG, Kachel NB, Sullivan ME. 2005. Observations from moorings in the Aleutian passes: temperature, salinity and transport. Fish. Oceanogr.14:39–54

Steer MA, Pecl GT, Moltschaniwskyj NA. 2003. Are bigger calamari *Sepioteuthis australis* hatchlings more likely to survive? A study based on statoliths dimensions. Mar Ecol Prog Ser 261:175-182

Tafur R, Villegas P, Rabi M, Yamashiro C. 2001. Dynamics of maturation, seasonality of reproduction and spawning grounds of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) in Peruvian waters. Fish Res 54:33-50

Van Heukelem WF. 1976. Growth, bioenergetics and life-span of *Octopus cyanea* and *Octopus maya.* Phd dissertation, University of Hawai'i, Honolulu

Wodinsky J. 1978. Feeding behavior of broody female *Octopus vulgaris*. Anim Behav 26:803-813

Yamashita Y. 1974. Spawning and hatching of *Paraoctopus dofleini* (Wülker). Monthly Rep of the Hokkaido Fish Exp Stat 31(7):10-22

Zghidi W, Ezzeddine-Najai S, Charfi-Cheikhrouha F, El Abed A. 2004. Reproduction of *Octopus vulgaris* Cuvier, 1797 in Gabes Gulf (Tunisia, Eastern Mediterranean Sea). Mar Life 14:31-36

CHAPTER SIX

Conclusion

General

This study has advanced the understanding of North Pacific giant octopus (*Enteroctopus dofleini*) biology and ecology in the eastern Bering Sea (EBS). Using Visible Implant Elastomer tags (VIEs), I examined how biotic and abiotic factors impact the growth, movement, survival and abundance of this species in a 25 km^2 study area 20 km northeast of Unalaska, AK. In Chapter 2, I examined the efficacy of using VIEs as a means to mark octopus for studying life-history attributes of this data poor species. In Chapter 3, I used mark-recapture information from the tagging study to determine if temperature, octopus size or sex could explain attributes of octopus growth and movement. In Chapter 4, I used Cormack-Jolly-Seber models to determine survival and abundance estimates in my study area. I then converted annual survival to an instantaneous mortality rate, and used federal fisheries observer data to estimate biomass in adjacent areas where most of the incidental commercial catch of octopus occurs in the EBS. In Chapter 5, I described sacrificing 195 individuals to determine if season, octopus size or sex could explain attributes of octopus maturity.

The results of this study fill in some of the gaps in the basic ecological knowledge of *E. dofleini* while providing fisheries managers with estimates of biomass and mortality. In Chapter 3, I show that growth and movement for *E. dofleini* increase with increasing temperatures which may be the result of increased food availability (Robinson and Hartwick 1986), metabolic rate (Rigby and Sakurai 2004) and conversion efficiency (Hartwick et al. 1981) associated with warmer temperatures. In Chapter 4, I show that density of octopus in my study area is two orders of magnitude higher than has been reported in nearshore areas of Prince William Sound

(Scheel 2002) and biomass may be one order of magnitude higher than the current estimate used by the Alaska Fisheries Science Center (Conners et al. 2014). I also show that survival for octopus in my study area is extremely low because large individuals tagged were likely mature and senescing within weeks to months (Chapter 4). Finally, in Chapter 5, I show that *E. dofleini* maturity in the EBS is seasonal with mating occurring in late autumn and spawning occurring in winter. The results of this study improve the knowledge of this species and can be used to guide future management under changing climate conditions.

Ecology and climate change

As many of the biological processes examined in this study are dependent upon temperature, climate change that results in a warmer ocean may alter ecological processes for *E. dofleini*. Increased temperatures may provide a larger potential prey base (Kanamaru 1979) and increase growth which could result in decreased predation risk in early life history stages (Mather and O'Dor 1991). Increased temperatures result in higher metabolic rates (Rigby and Sakurai 2004) that generally required an increased feeding rate for growth and survival (Borer and Lane 1971). Increased temperatures could also result in greater total growth, a larger size for mature females, and an increase in the number of eggs produced (Kanamaru 1979); however higher metabolic rates may also mean increased energy required for mate searching (Chapter 3). Faster growth and larger size *E. dofleini* with warmer temperatures has been speculated as a reason why *E. dofleini* reach a larger overall size and size at maturity at the southern extent of its range (Robinson 1983). Ocean warming may also decrease the time for *E. dofleini* eggs to hatch (Kubodera 1991) which may cause a match-mismatch in the timing of the spring phytoplankton bloom (Chapter 5).

Fisheries Management

This biological study provides attributes that relate to fisheries and may prove useful in fisheries management. Cephalopods in general are difficult to manage because of their short life spans and semelparous reproductive strategy, as well as the difficulty of accurately assessing their age. As fisheries management depends on biological information to model populations, limited information can hinder assessments. In this study, growth, movement, reproduction and biomass estimates may prove useful in supplementing population modeling efforts for octopus in Alaska.

In the Bering Sea/Aleutian Islands (BSAI), eight species of octopus are managed as a complex by the North Pacific Fisheries Management Council. Due to a lack of information, octopus are managed using the most conservative approach (Tier 6), which sets annual limits using historical catch data. Tier 5 management requires accurate assessment of biomass (B) and mortality (M), which are currently unreliable for octopus in Alaska. The only estimates for octopus biomass in the BSAI come from federal bottom trawl surveys which may not be appropriate for a highly mobile species that can avoid trawls and lives in rocky substrates that are problematic for trawl gear. Though annual mortality for *E. dofleini* has been estimated using Rikhter and Efanov's (1976) equation, the value of M = 0.53 is based upon an age of maturity of three years, despite no proven methods to age *E. dofleini* (Conners et al. 2014). In 2014, federal fisheries managers set annual catch limits using a consumption-based estimate of octopus by Pacific cod (*Gadus macrocephalus*). Using the consumption-based estimate as a biological reference point for total natural mortality (N), federal fisheries managers combined N with a general logistic fisheries model to set the over fishing limit (OFL) at the estimate of mortality.

This approach is problematic because Pacific cod represent only one of many octopus predators, octopus beaks found in Pacific cod stomachs are juveniles (< 2 kg body weight), and samples were taken only during summer months. Though the consumption estimate represents an option for managing this data poor complex, I believe the study presented here will enhance our ability to manage octopus in Alaska.

In this study, estimates of B and M were a result of sampling both the size of octopus and the spatial region where most of the catch of octopus occurs. The biomass and mortality estimates presented here are the result of directed studies on octopus and not tangential information of potential predators or estimated age at maturity. The biomass estimate of 20,697 mt for federal management areas 509, 517 and 519 is based upon a combination of this tag and recapture effort and 20 years of federal observer data. The annual mortality estimates were high, 3.4 compared to 0.56, though consistent with the majority of tagged octopus being mature and likely senescing. Semelparity and high annual mortality in mature individuals indicate that annual mortality may not be the most appropriate parameter to assess octopus populations, particularly the proportion susceptible to incidental capture.

As a result of this study, I make the following three recommendations to federal fisheries managers:

1) As 82% of *E. dofleini* observed in the study area were mature and likely senescing and dying within months, I suggest using 0.82 * 20,697 mt (the estimated biomass for areas 509, 517 and 519) as a biological reference point for natural mortality and set the OFL = 16,972 mt and the acceptable biological catch (ABC) = 0.75 * OFL = 12,729 mt. As the 16,972 mt of octopus are likely going to senesce and die anyway and as the 3,500 km^2 area of 509, 517, and 519 represent a fraction of the EBS area, this would still offer

management a conservative catch limit and is in line with the current model for estimating natural mortality.

2) Because the mortality estimate in this study applies primarily to mature octopus, it may not be applicable to octopus throughout their lifecycle. In that case, the Rikhter and Efanov estimate of $M = 0.53$ may be more precautionary, resulting in a Tier 5 OFL = $M * B = 0.53 * 20.697$ mt = 10,969 mt and an ABC = 0.75 * OFL = 8,227 mt.

3) As this study has shown that growth, movement and proportion of mature octopus are highest during autumn months, effort controls (i.e., time or area closures) may be an effective option for future management. Effort controls have been used in Morocco and Japan, where octopus fishing is limited by season (www.globefish.org; Mottet 1975), and in British Columbia, where octopus fishing is limited by management area (Fisheries and Oceans Canada 2005). Reduced retention of female *E. dofleini* during autumn months may ensure they have the potential to mate and spawn (Chapter 5).

Though there are a variety of regulatory approaches for invertebrate species, in the long term, sustainable management must be an adaptive process that incorporates information gathering, reassessment of stock viability, and adjustment of harvest policy (Perry et al. 1999).

Future studies

Though this study provides major insights to the biology and ecology of this species, future research is needed to enhance knowledge of *E. dofleini* over broader scales. To expand upon the results presented here, a larger temporal and spatial scale study using VIEs would provide information on the abundance and distribution of *E. dofleini* at a greater scale. Perhaps an intensive assessment of *E. dofleini* in federal management areas 509, 517 and 519, where

most of the commercial incidental harvest of *E. dofleini* occurs. By using the tag and recapture protocols described in this study and expanding those types of efforts to other federal observer 400 km^2 blocks, fisheries managers would have more density estimates to compare to observer catch effort data, hence supporting or refuting the biomass estimates reported in this study.

The Alaska Fisheries Science Center has recently begun creating large-scale maps of species distributions using predictive habitat modeling to link habitat and oceanographic parameters with information from federal fisheries observers (N. Laman, personal communication). Combining predictive habitat maps with catch-based density estimates may allow estimation of *E. dofleini* abundance across larger spatial scales.

In this study, I provide estimates of biomass and mortality for a primarily mature proportion of octopus in the study area. As *E. dofleini* are thought to live at least three years (Kanamaru 1979), it is likely that in any given year there are multiple cohorts in the same environment. To better quantify octopus biomass and mortality at all life stages, I would recommend using different gear types to evaluate octopus at different life stages. As *E. dofleini* are known to select dens based upon their size (Hartwick et al. 1978), size-specific octopus traps could be used to capture and tag smaller *E. dofleini* to better understand the immature portion of octopus populations.

Finally, very little is known about the early life history of *E. dofleini,* from hatching paralarvae to settlement stage. Seasonal plankton tows in the Aleutian Islands suggest that *E. dofleini* paralarvae peak in abundance from late spring to early summer (Kubodera 1991) though surface tows were limited in space and time. Laboratory studies of paralarval growth and settlement with temperature will provide information on the timing of settlement and survival of

juvenile bethnic *E. dofleini* with ocean warming. Paralarval success may drive population viability and may determine year to year variability.

Considering that *E. dofleini* represent a large incidental catch in commercial fisheries and may one day prove suitable for a directed fishery, understanding biological and ecological attributes at appropriate scales is important to sound fisheries management. Though there are still gaps in our knowledge of *E. dofleini* life-history, this study provides pertinent and representative data about the octopus that are incidentally caught in Alaska and may serve as a reference point for future studies.

LITERATURE CITED

Borer KT, Lane CE. 1971. Oxygen requirements of *Octopus briareus* (Robson) at different temperatures and oxygen concentrations. J Exp Mar Biol and Ecol 7: 263-269

Conners ME, Conrath C, Aydin K. 2014. Assessment of the Octopus Stock Complex in the Bering Sea and Aleutian Islands. North Pac Fish Mgmt Council, Anchorage, AK

Fisheries and Oceans Canada. 2005. Pacific Region Octopus by Dive Experimental Harvest Guidelines. August 1, 2005 to July 31, 2006. 21pp

Hartwick EB, Breen PA, Tulloch L. 1978. A removal experiment with *Octopus dofleini* (Wülker). J Fish Res Board Can 35:1492-1495. doi: 10.1139/f78-235

Hartwick EB, Tulloch L, MacDonald S. 1981. Feeding and growth of *Octopus dofleini*. Veliger 24:129-138

Kanamaru S. 1979. The life of paroctopus hongkongensis and the species of octopuses along the Rumoi Coast, Hokkaido. Fisheries and Marine Service Translation Series No. 4528. 36 pp

Kubodera T. 1991. Distribution and abundance of the early life stages of octopus, *Octopus dofleini* in the North Pacific. Bull Mar Sci 49:235-243

Mather JA, O'Dor RK. 1991. Foraging strategies and predation risk shape the natural history of Juvenile *Octopus vulgaris*. Bull Mar Sci 49(1-2):256-269

Mottet MG. 1975. A technical report on the fishery biology of *Octopus dofleini*. Washington Department of Fisheries, Tech Rep. No 16, 38p

Perry RI, Walters CJ, Boutillier JA. 1999. A framework for providing scientific advice for the management of new and developing invertebrate fisheries. Rev Fish Biol Fisheries 9:125-150

Rigby PR, Sakurai Y. 2004. Temperature and feeding related growth efficiency of immature octopuses *Enteroctopus dofleini*. Suisanzoshoku 52(1):29-36

Rikhter VA, Efanov VN. 1976. On one of the approaches to estimation of natural mortality of fish populations. ICNAF Res. Doc., 79/VI/8

Robinson SMC. 1983. Growth of the giant Pacific octopus (*Octopus dofleini martini*) on the west coast of British Columbia. MS thesis, Simon Fraser University, Canada

Robinson SMC, Hartwick EB. 1986. Analysis of growth based on tag-recapture of the giant Pacific octopus (*Octopus dofleini martini*). J Zool 209:559-572

Scheel D. 2002. Characteristics of habitats used by *Enteroctopus dofleini* in Prince William Sound and Cook Inlet, Alaska. Mar Ecol 23(3):185-20